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Author(s): Paul K. Dayton, Mia J. Tegner, Peter B. Edwards and Kristin L. Riser

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TEMPORAL AND SPATIAL SCALES OF KELP DEMOGRAPHY: THE ROLE OF OCEANOGRAPHIC CLIMATE

PAUL K. DAYTON,¹ MIA J. TEGNER, PETER B. EDWARDS, AND KRISTIN L. RISER

Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California 92093-0201 USA

Abstract. This paper integrates long-term descriptive and experimental studies of the effects of ocean climate on inter- and intraspecific competition, as expressed by recruitment, density, survivorship, growth, and reproduction of the most conspicuous kelp species in the Point Loma kelp forest community off San Diego, California, USA. The species included *Macrocystis pyrifera*, with a floating canopy; *Pterygophora californica* and *Eisenia arborea*, which rely on stipes to support their canopy; *Laminaria farlowii*, with a prostrate canopy; and a speciose red algal turf. To evaluate the roles of large-scale oceanographic processes on biological processes across important depth gradients, the study was carried out over nine years during a cold-water, nutrient-rich La Niña event (1988–1989) and a warm-water, nutrient-stressed El Niño period (1992–1994), over a depth range of 8–23 m. This depth range encompassed strong physical gradients involving factors that are critical for kelp growth, including bottom temperatures (correlated with nutrients) and light levels.

To examine interactions among these kelps, we established clearings across the depth gradient and then manipulated *Macrocystis* recruit densities. The demographic responses offer an understanding of the “fundamental” vs. “realized” niches of these species. Evaluating these patterns, as they are influenced by inter- and intraspecific competition, offers insights into the “realized niches” of the kelps. With the exception of some understory effects on *Macrocystis* recruitment and some evidence of intraspecific competition during the nutrient-rich La Niña conditions, we found little influence of competitive effects on *Macrocystis*. The response of *Pterygophora* to manipulations and disturbances suggests light-limited recruitment, and competition with *Macrocystis* was exhibited via reduced growth and reproduction, but not survivorship. No nutrient stress was observed in *Pterygophora* reproduction. *Eisenia* recruitment is rare, but once established, juveniles had very good survivorship, with growth and reproduction reduced by depth; the *Macrocystis* treatment was more important than depth, suggesting the importance of light to *Eisenia* recruitment and growth. In general, *Macrocystis* had massive effects on *Laminaria* growth and reproduction, the strength varying with depth. In particular, there were very strong effects of competition with *Macrocystis* during the nutrient-rich La Niña period when *Macrocystis* had a dense surface canopy. In addition to the *Macrocystis* effects, there were some significant *Pterygophora* effects on *Laminaria* growth during El Niño.

The strongest biological definition of realized niches occurred during the nutrient-rich La Niña period, especially in shallow depths. One of the most important conclusions of this paper is the appreciation of the importance of scaling in time to include oceanographic climate. There are many seasonal patterns, but the interannual scales that encompass El Niños and La Niñas, and ultimately the interdecadal-scale oceanographic regime shifts that affect the intensity of canopy competition with *Macrocystis*, are critical for this system because surface-water nutrients have pervasive long-term effects on the other kelps. Small-scale patterns are driven by local processes (competition, disturbance, dispersal, etc.) that potentially are important at larger scales; however, our most lasting effects result from very large-scale, low-frequency episodic changes in nutrients, with cascading competitive consequences to the other algal populations in the community.

Key words: community structure and competition; depth gradient; *Eisenia*; El Niño and La Niña events; kelp; *Laminaria*; *Macrocystis*; fundamental vs. realized niches; ocean climate; *Pterygophora*; scaling up small-scale research; time scales.

INTRODUCTION

Most important issues in community ecology involve the evaluation of scale-dependent relationships among

populations and communities. In coastal habitats, the spatial variability involves the depth distribution of the species, and temporal variability involves evaluating important processes over many years and even decades during different oceanographic conditions. Do disturbances, nonequilibrium conditions, or large-scale episodic events override equilibrium mechanisms in

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¹ E-mail: pdayton@ucsd.edu

structuring communities? What is the role of the frequency and intensity of competition as it affects comparison between density dependent/independent population control and density-vague (Strong 1986) relationships? Most important population and community processes also involve the trade-off between inter- and intraspecific competition, and the roles of disturbance and succession in population dynamics and community organization. Obviously, these processes are integrated in nature, and clarifying this integration contributes to understanding the organization of biological communities, as well as to a better perception of evolutionary processes that structure coastal communities. Finally, how do ecosystem processes, such as the control of productivity and various rate processes, influence these evolutionary processes?

An earlier paper (Tegner et al. 1997) demonstrated that the equilibrium conditions that dominated after massive El Niño and storm disturbances failed to persist through a La Niña that stimulated strong competitive dominance. This paper addresses the effects of competition and oceanographic climate across a depth gradient as they influence patterns of density, survivorship, growth, and reproduction of the most conspicuous kelp species in the Point Loma kelp forest community off San Diego, California, USA. We integrate long-term descriptive and experimental data and specifically address effects of inter- and intraspecific kelp density on these parameters in different depths and years, integrating time and space with an evaluation of the roles of large-scale oceanographic processes. We contrast small-scale patterns driven by processes (competition, disturbance, dispersal, etc.) that are also potentially very important at larger scales; however, we ask whether the most lasting effects result from very large-scale, low-frequency episodic changes in the oceanographic climate.

Scales.—Understanding stability of patterns in time and space always has been a dominant theme in ecology. Ecologists have become acutely attuned to the problems of replication in study design at small scales, as well as the scale dependence of inferences derived from experimental hypothesis testing (Schneider et al. 1997, Thrush et al. 1997). Only rarely are research scales explicitly chosen to be appropriate to the questions, and, despite the fact that it is increasingly apparent that many important processes take place over longer and larger scales, most ecologists tend to avoid environmental heterogeneity and work at ever smaller and more homogeneous plots, enhancing the precision of their experiments at the cost of their generality. McGowan (1995) reviews long-term studies of marine populations where large-scale, interannual and interdecadal changes in abundance account for most of the variability in these communities. Bascompte and Sole (1995) review the chaotic behavior of many temporal population models as influenced by the stabilizing effect of spatial heterogeneity. However, ecological re-

search seems to focus on oscillations and extinctions of small local populations, without making explicit reference to the larger scales in space and time; often populations behave very differently at these larger scales. Very few marine situations are relevant to the type of metapopulation dynamics reviewed by Bascompte and Sole (1995), because local extinctions of patches of individuals are very small scale and clearly do not constitute populations in the normal sense. Certainly there are local differences in survivorship, but, in fact, most population interactions do not result in extinctions of metapopulations, although they may still have important influence on various demographic factors such as age-specific rates of growth and reproduction.

Environmental gradients.—Most communities and their component populations exist along environmental gradients. The definition of such continua has been a productive component of terrestrial ecology (see McIntosh 1995), but there is a tendency to focus on obvious zonation in marine systems; the gradients usually include depth or wave exposure, and the strata are tested against a null continuum model, with the main objective of defining mechanisms causing discontinuities or zonation. Because they are mechanistic and often involve elegant experiments, such studies represent some of the best-known paradigms of benthic ecology (Paine 1994). There are few attempts to go beyond the zonation and integrate intra- and interspecific density effects across a gradient, although Dayton (1975a, b) found striking interspecific effects that were strongly affected by depth and wave exposure gradients in Washington and Alaska, as well as in California kelp forests (Dayton et al. 1984, 1992). Novacek (1984) observed striking reproductive differences in *Ecklonia radiata* at 7–15 m depths in New Zealand. In central California, Harrold et al. (1988) and Graham et al. (1997) described the effects of a gradient of wave exposure on kelp species structure and population dynamics, respectively. Foster (1990) pointed out the paucity of kelp studies along the complete depth gradient over which they occur. Nevertheless, even fewer of these studies considered intraspecific effects or evaluated growth and reproduction across the gradient.

Competition.—Some of the earliest ecological theory was built on a clear understanding of the importance of both inter- and intraspecific competition as well as predation (Gause 1934). The effects of inter- and intraspecific competition are important to community and evolutionary theory, even if they occur in a density-vague manner (*sensu* Strong 1986). Studies of canopy competition are common in kelp forest research (and include some of the earliest, such as Hatton [1932], Kitching et al. [1934], Kitching [1941]). Much of this research has been reviewed by Dayton (1985), Schiel and Foster (1986), Chapman (1986b), and DeWreede and Klinger (1988). Despite this long-standing interest, uncertainty exists about density effects on

algal productivity, and this is particularly true across depth gradients (Brawley and Adey 1981, Schiel and Choat 1981, Cousins and Hutchins 1983, Schiel 1985). Different interpretations may result from confounding differences in plant architecture or habitat structure or depth. Santelices (1990) reviews studies of intra- and interspecific effects on reproduction and recruitment.

Disturbance.—Most reviews of disturbance have emphasized the importance of the intensity and scales of the perturbation. Kelp forests are exposed to a large array of disturbances, from small to large scales, that usually results in patchiness (Dayton et al. 1984, 1992). Such patchy structure can be removed by sea urchin grazing (Harrold and Pearse 1987). Kelp forest communities are also influenced by much larger scale physical processes that, in our case, involve the entire Southern California Bight and the much larger California Current system. Oceanic and atmospheric processes in the Pacific cause large-scale, low-frequency changes leading to important interannual variability, such as El Niños and La Niñas. These and smaller mesoscale (1–100s of km) oceanic anomalies are responsible for many episodic events that have long-term implications (Tegner and Dayton 1987, Dayton and Tegner 1990, Dayton et al. 1992). The persistence of such postdisturbance states in kelp forests vary. Some Alaskan urchin barrens appear persistent so long as sea otters are rare or absent (Simenstad et al. 1978, Duggins et al. 1989), while extensive Nova Scotia urchin barrens were stable for a decade until disease killed the urchins (see reviews in Chapman and Johnson 1990, Elner and Vadas 1990, Vadas and Steneck 1995). Other kelp habitats in the Gulf of Maine depend upon a bivalve substrate that is vulnerable to various types of disturbances (Witman 1987). The 1957–1959 El Niño in southern California was associated with sea urchin barrens that recovered quickly, without management, in nonpolluted areas (R. McPeak and W. J. North, *personal communication*), while recovery varied from a few years at Point Loma to a score of years in Los Angeles County (Wilson et al. 1977). Two very unusual and massive large-scale storm disturbances (associated with the most intense El Niño in a century and an apparent 200-yr storm; Seymour et al. 1989) impacted the Point Loma kelp forest in the 1980s; one effect was increased canopy destruction, but much of the structure of the community recovered quickly (Dayton et al. 1992). Tegner et al. (1997) considered the important secondary effects of large disturbances followed by different oceanographic climate events and found striking differences in succession driven by the density and condition of the *Macrocystis* canopy and its competitive effects on understory populations.

Prioritizing environmental variables

Which environmental factors define patterns of distribution and abundance of kelps across a gradient? We used Hutchinson's (1957) niche theory to prioritize the

importance of potential explanatory variables over different spatial and temporal scales. Physical factors affecting plants include temperature, nutrients, light quality and quantity, wave exposure, and sediments. Such factors potentially determine patterns of recruitment, survivorship, growth, and reproduction; as such they define the "fundamental niches" (sensu Hutchinson 1957) of the species. Within the context of actual kelp communities, fundamental niches may be importantly modified by biological processes, especially intra- and interspecific competition and disturbances including grazing, abrasion by plants, or other interactions that impose restrictions beyond those of the physiological limits (Dayton 1975a). There are also many indirect negative interactions such as canopy reduction of nutrients and modification of flow regimes (Jackson 1977, Jackson and Winant 1983, Eckman et al. 1989), and there probably are indirect positive effects as well (e.g., Witman 1987, Bertness and Callaway 1994). Hutchinson termed these distribution patterns "realized niches." Yet, as with most actual communities, patterns in kelp forests are patchy in space and variable in time. We attempt to compare these heterogeneities to the general importance of biological processes. To do this, we evaluated aspects of fundamental and realized niches of the dominant kelp species as they are influenced by the two most important environmental factors: water depth and density of the canopy forming plants. In this system, the role of depth encompasses gradients in light, wave energy, and temperature (a surrogate for nutrient availability).

Our identification of critical variables is based on earlier studies of temporal and spatial patterns of disturbance and recovery (Dayton et al. 1992), evidence for the effects of a long-term oceanographic regime shift (Tegner et al. 1996), direct and indirect effects of gradients of wave exposure on competitive and successional patterns (Dayton et al. 1984), and ecologically important shifts in competitive relationships during different oceanographic climate conditions (Tegner et al. 1997). Here we report on controlled experiments evaluating the relative effects of *Macrocystis pyrifera* canopy on the density, growth, and reproduction of *Pterygophora californica*, *Eisenia arborea*, and *Laminaria farlowii*. For *Macrocystis* and *Pterygophora* we also evaluated the effects of manipulating intraspecific density. We attempted to control for or measure other variables: temperature, light, grazing, and, by choice of sites, substrata differences. Recent experiments are put in context of work done in the 1970s and 1980s, and we report new data on density, growth, and reproductive processes during two very different oceanographic climate events (Hayward et al. 1994, 1995): a nutrient-rich La Niña event (Kerr 1988) in 1988–1989 and nutrient-stressed El Niño conditions in 1992–1994. Clearly this program is similar to benthic programs, especially diving ones, that often lack adequate data for sophisticated analysis (Legendre et al. 1997,

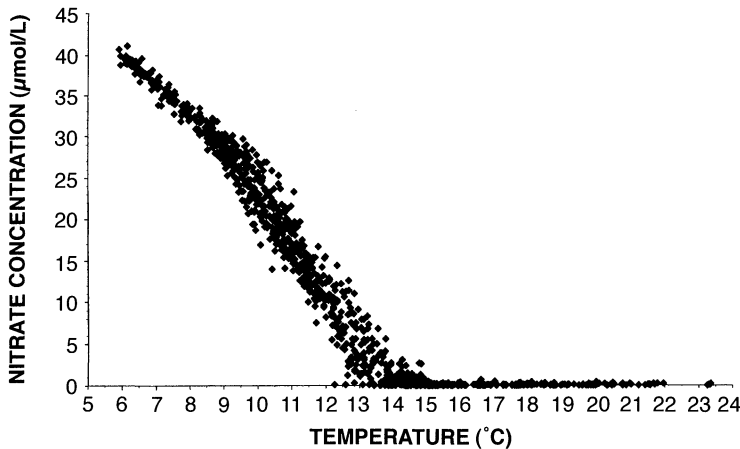


FIG. 1. Temperature vs. nitrate relationship from hydrocasts made quarterly by the California Cooperative Oceanic Fisheries Investigations program, 1986–1996, from three inshore stations off Del Mar, California (117.1–117.4° W, 32.5–33.0° N), the closest sites to Point Loma, California. Water samples were taken from the surface to 400 m. (For details, see Scripps Institution of Oceanography [1994].)

Schneider et al. 1997), but we have studied sufficient scales in space to evaluate commonly accepted generalizations of canopy effects in this one kelp forest, and this may be the only such study repeated through sufficient time to assess differences in interannual oceanographic variability.

SITE AND SPECIES DESCRIPTIONS

This paper is based on work done in the Point Loma kelp forest off San Diego, California, USA. Research from the mid-1950s by W. J. North and M. Neushul, and our own work starting in 1970, are summarized in Tegner et al. (1996, 1997). The kelp forest is ~8–10 km long \times ~1 km wide. It is one of the largest giant kelp forests in the world, and it has marked cross- and long-shore gradients. We have maintained long-term study sites in different areas of the kelp forest since 1971 (Dayton et al. 1992), with the intention of integrating gradients in important environmental factors such as depth, light, nutrients, wave energy, flow, planktonic propagules, and epifaunal animals. In January 1988, an extremely violent storm struck San Diego and produced extraordinary biological and physical damage at Point Loma (Dayton et al. 1989, Seymour 1989, Seymour et al. 1989).

Kelp forests are composed of canopy types that can be categorized into guilds distinguished by morphological adaptations (Dayton 1985). In southern California, these include the following features: (1) a floating canopy (*Macrocystis*), (2) an erect understory in which the fronds are supported by stipes (*Pterygophora californica* and *Eisenia arborea*), (3) a prostrate canopy lying on the substratum (*Laminaria farlowii*), (4) a turf composed of many species of foliose and articulated coralline algae, and (5) a pavement of encrusting algae.

Kelps occur from the intertidal zone to depths \gg 25 m, and species composition changes along this gradient (see Dayton et al. 1992). Competitive relationships among kelps at Point Loma are well described (Dayton et al. 1984, 1992, Tegner et al. 1997). The dominant kelp, *Macrocystis pyrifera*, which provides most of the

structure and primary productivity, ranges in depth 5–25 m. *Pterygophora californica* is most abundant in waters $<$ 15 m (Dayton et al. 1992). *Laminaria farlowii* is also a common and important understory species in southern California; it has an extremely wide depth distribution occurring from the intertidal to 120 m (Lissner and Dorsey 1986). *Eisenia arborea* offers another interesting pattern, in that it is found on rocky outcrops as deep as 40 m, yet it occurs all the way into the intertidal at Point Loma. Previous work (Dayton et al. 1984) has shown a competitive hierarchy of *Macrocystis* $>$ *Pterygophora* $>$ *Laminaria* and the other understory algae including red foliose and coralline algae, with an inverse hierarchy of susceptibility to wave stress. *Macrocystis* is subjected to sustainable harvest that has no measurable negative impacts on kelp population parameters. We have no evidence that the kelp populations at this location, their interactions, and their responses to the oceanographic patterns generally are much affected by anthropogenic influences.

Nutrient distributions in southern California are strongly affected by density stratification and occasionally by uptake and release by phytoplankton. As temperature is the dominant factor controlling sea water density in this region, there is a clear relationship between temperature and nutrient concentrations, and the processes that affect density and temperature, such as shoaling of isotherms near the coast, wind-driven upwelling or downwelling, and internal waves, also affect nutrient distributions (Eppley et al. 1979, Jackson 1983). A strong negative correlation between temperature and nitrate, the nutrient most likely to limit kelp growth (North et al. 1982), has been established for the southern California Bight; there are negligible amounts of nitrate for temperatures $>$ 15°C (Jackson 1977, 1983, Gerard 1982, Zimmerman and Kremer 1984). Fig. 1 illustrates a 10-yr temperature vs. nitrate relationship from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) station nearest to the Point Loma kelp forest. The same relationship for the Point Loma kelp forest (Jackson 1977) shows a

similar slope and intercept but more variation, which probably relates to the influence of the bottom and the far higher abundance of animals than in open water. The relationship tends to be temporally stable, although there is some noise that may be related to the advection of different water parcels (Zimmerman and Kremer 1984), or to the use by phytoplankton, which leads to lower nitrate concentration coupled with high oxygen and chlorophyll with little temperature change (Hayward and Mantyla 1990). Zimmerman and Robertson (1985) found a slight but significant variation at Santa Catalina Island in the temperature vs. nitrate relationship between non-El Niño conditions (1981) and a strong El Niño year; the intercept shifted slightly but the slope of the relationship was not changed. We compared the temperature at which regression lines indicated zero nitrate and found slight shifts as well: for the 1986–1996 period, the value was 14.3°C; for the 1988–1989 La Niña period, the value was 14.2°C; and for the 1992–1994 El Niño period, the value was 14.5°C. Schroeter et al. (1995) present evidence that the higher nutrient concentrations within a few centimeters of the bottom, presumably from regeneration in the sediments or animal excretion, aided the growth of blade stage *Macrocystis* in 1983. As multifrond juvenile kelps (>1 m) grew slowly and were experimentally shown to be nutrient limited (Dean and Jacobsen 1986), they concluded that temperature is a useful proxy for nutrient concentrations in the water column, but not for benthos.

Average in situ water temperatures at Point Loma decrease significantly with depth in the cross-shore direction, with 12-, 15-, and 18-m depths all significantly different from one another (Dayton et al. 1992). Seasonally, bottom and surface temperatures follow different patterns, with the coldest bottom water in the spring/early summer, followed by rising temperatures in the late summer/fall, and an isothermal water column in the winter. Both surface and bottom temperatures are strongly correlated with sea level, and >75% of the variance in sea level in the southern California Bight is accounted for by equatorial forcing by El Niño–Southern Oscillation (ENSO) events (see Tegner et al. 1996). Interannual variability in recent years has been dominated by the 1982–1984 El Niño, considered to be the strongest observed to that time, the 1988–1989 La Niña, a cold-water ENSO event, and strong but intermittent El Niño conditions during 1992–1993. Using a 31-yr database for kelp harvest, Tegner et al. (1996) found that the best predictor of annual kelp harvest among several physical variables was average surface temperature. This correlation results from the fact that most of the biomass and most of the production of giant kelp is in the surface canopy; this high proportion of *Macrocystis* above the thermocline probably overwhelms the capacity for upward nutrient transport.

Light patterns in the Point Loma kelp forest vary considerably with depth, runoff, wave surge, plankton

populations, other dissolved or particulate material in the water, shading by attached organisms, and surface light level. In the absence of other factors, such as grazing or unsuitable habitat, the lower depth limit of the kelp forest is apparently set by light (reviewed by Foster and Schiel 1985). Lunning (1981) suggested that this limit occurs at ~1% of surface irradiance for most kelps. Light is attenuated logarithmically with depth; the extinction coefficient varies inversely with turbidity. Both *Macrocystis* and *Pterygophora* canopies can reduce benthic irradiance levels by 90%, relative to kelp-free areas at the same depth (Reed and Foster 1984).

Some of the worst water conditions we have seen in >25 yr of work at Point Loma occurred in winter 1993, which was characterized by 190% of the average (1939–1992) number of rainy days, vs. 45% for 1988. Muddy runoff resulted in extremely poor water visibility. The visibility cleared somewhat during spring, but there was a thick plankton bloom over the entire region. Our observations of massive plankton blooms in the kelp forest were associated with measurements of low light availability on the bottom and low kelp recruitment during this period. This extended period of low light may have been responsible for the very poor kelp recruitment during this time, relative to 1988. However, there were no major wave events during this period, so large-scale spore dispersal was likely to be limited (Dayton et al. 1984, Reed et al. 1988). Heavy suppression of the understory by the strong *Macrocystis* canopy during the La Niña may also have contributed to the low understory kelp recruitment observed in 1993 (Tegner et al. 1997).

MATERIALS AND METHODS

Monitoring important physical variables

Temperature.—We have continuously measured bottom temperatures, at our study sites of 8, 12, 15, 18, and 21 m, using Ryan TempMentors (Ryan Instruments, Redmond, Washington, USA) and StowAway data loggers (Onset Instruments, Pocasset, Massachusetts, USA). Monthly temperature means were calculated using 8 values/d. Sea surface temperature data are from the Scripps Institution of Oceanography (SIO) pier, 17 km north of the study sites. A diving quarantine during the 1992 sewage spill and equipment failures caused several gaps in the data. Previously published temperature data (Dayton et al. 1992, Tegner et al. 1996) are updated for reference (Fig. 2A).

Irradiance.—During December 1989–December 1991, six Li-Cor Quantum sensors (LI-192SB) with Micro-Powered underwater data loggers (model UDL 250-3, ECOSystems Management Associates, Encinitas, California, USA) were deployed ~22 d each month in the high and low density *Macrocystis* treatments at 8, 15, and 21 m. Irradiance at the bottom was integrated over 15 min periods and stored in erasable program-

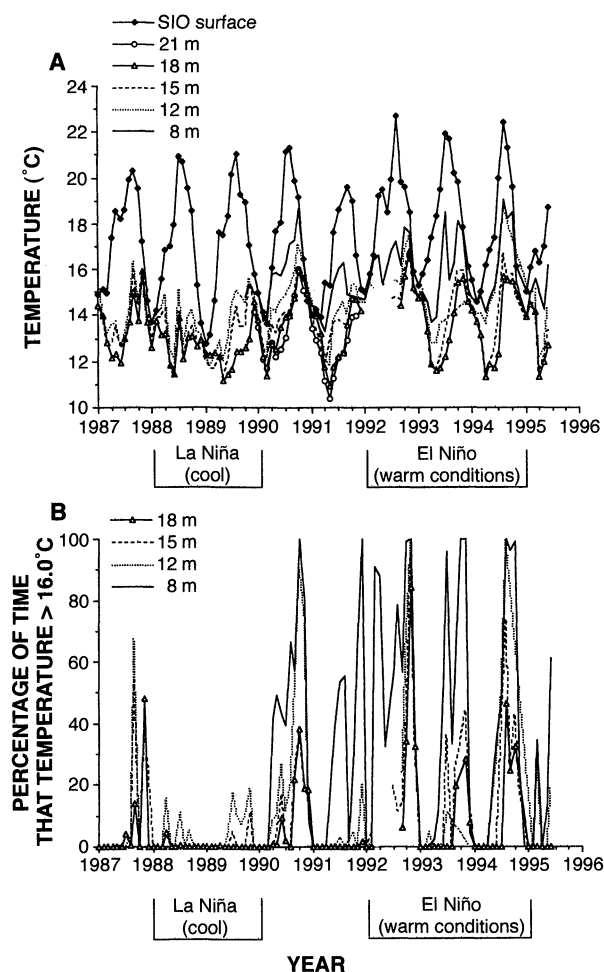


FIG. 2. (A) In situ bottom temperatures, from 8-, 12-, 15-, 18-, and 21-m depths, in the center of the Point Loma kelp forest and the surface temperature from the Scripps Institution of Oceanography (SIO) pier, ~17 km to the north, 1987–1995. (B) Percentage of the observations (8 observations/d) each month in which bottom temperatures were above the 16°C nutrient threshold (NO_3^- concentration is negligible at temperatures higher than this) at three sites in the center of the forest. The data gaps during 1992 were due to a large sewage spill, during which we were not able to deploy and retrieve instruments.

mable read-only memory (EPROM) units; total daily levels were calculated from these values. While accurate, these instruments proved unreliable and the data sets were incomplete (Fig. 3). Irradiance data were collected again with the same instruments in March and April 1993 in the *Macrocystis* exclusion treatments at the 8- and 15-m sites (Fig. 4).

Permanent transects.—In 1971 we established non-replicated transects at 12-, 15-, and 18-m depths in the central region of the Point Loma kelp forest, and these were replaced in 1983 with replicates at each site. At each site, four parallel 25-m lead lines were installed in an onshore–offshore direction, with the lines spaced

5–7 m apart. The plants were mapped (on a grid basis; see Dayton et al. 1984) quarterly within 2 m of each side of each line (400 m²/site). All *Macrocystis* with ≥ 4 stipes were mapped, as were the understory species when possible. We also usually estimated percent cover of *Laminaria* and turf algae on a quarterly basis (Dayton et al. 1992, Tegner et al. 1996, 1997).

1988 clearings.—In winter 1988, immediately following the storm, we initiated an experiment to determine the effects of kelp density (inter- and intraspecific) on competitive relationships. To evaluate effects across a depth gradient, experiments were established at 8, 15, and 21 m in a cross-shore transect in the central region of the Point Loma kelp forest. At each depth, all nonencrusting macroalgae and urchins were cleared from one 30 × 30 m area. To avoid edge effects, the experiments were conducted within the central 20 × 20 m. Lead lines marked the boundaries of the squares. To evaluate effects of different densities of *Macrocystis*, we manipulated them such that half (20 × 10 m) had a naturally recruited ambient density and the other half of the clearing had the *Macrocystis* density reduced to one-third (low density) of natural density. Kelp density data were collected until spring 1991. Algal populations in the clearings were assessed quarterly. All kelps were counted and percent cover of turf algae estimated within 2 m of the three permanent lines crossing the treatments of each clearing.

1993 clearings.—In winter 1993, we again cleared the same (1988) areas of all macroalgae and sea urchins, but also made several modifications to the 1988 design. First, an additional treatment was added to examine growth and competition of understory kelp species in the absence of *Macrocystis*. The clearings were expanded and now measured 30 × 20 m; one-third of each clearing (10 × 20 m) had one of the following treatments: (1) a naturally recruited density of *Macrocystis* (high density), (2) a density of *Macrocystis* one-third of naturally recruited density (low density), and (3) complete removal of *Macrocystis* (no *Macrocystis*). To eliminate edge effects, a 10-m buffer zone around the entire clearing was maintained free of *Macrocystis*. To examine recruitment and competition among species of kelps at the extreme depth range of *Macrocystis*, an additional 30 × 20 m clearing was made at 23 m, where *Macrocystis* naturally occurs in relatively low density. To examine spatial variability on a small scale, an additional 30 × 20 m clearing was made at each depth, with distances between the two clearings ranging from 30–50 m, with the exact location chosen to match substrates and natural kelp populations of the preexisting clearings. In winter 1995, a powerful storm with a maximum significant wave high of 5 m (Coastal Data Information Project, SIO) greatly reduced the number of *Macrocystis* at our study sites, leading to the decision to terminate the study.

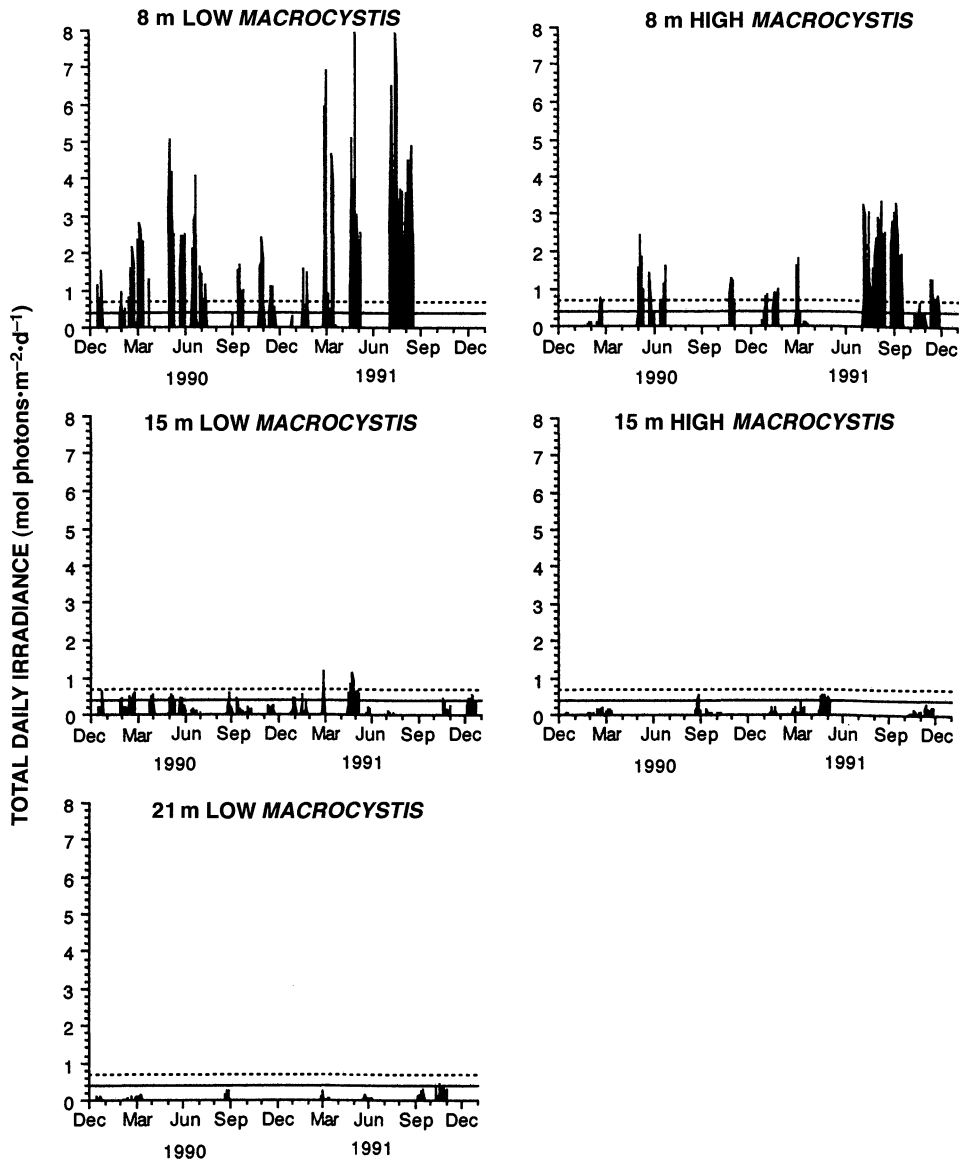


FIG. 3. Total daily irradiance on the bottom, December 1989–December 1991. Irradiance was recorded in the high-density (“HIGH”) and low-density (“LOW”) *Macrocystis* treatments at 8 and 15 m, and in only the low-density *Macrocystis* treatment at 21 m; data were recorded ~22 d/mo.

Tagged kelp plants

To study intra- and interspecific effects on growth and reproduction in the different treatments, we tagged individual *Macrocystis*, *Pterygophora*, *Eisenia*, and *Laminaria* plants. The giant kelps were tagged with plastic-coated wire that was looped around haptera, and the tags were replaced as they were overgrown; stipitate plants were tagged with Floy spaghetti tags tied on the stipes. In 1988, 20 *Macrocystis* were tagged in each treatment at 8 and 15 m, but only 10 were tagged in each treatment at 21 m, because of low recruitment. Twenty *Pterygophora* were tagged in each treatment at 8 and 15 m, but there was no recruitment at 21 m. Fifteen *Laminaria* were tagged in each treatment at 8,

15, and 21 m. In late 1990, there was recruitment of *Eisenia* in the low *Macrocystis* treatments at 8 and 15 m; seven *Eisenia* were tagged at 15 m, and six were tagged at 8 m.

In 1993, *Macrocystis*, *Pterygophora*, and *Laminaria* recruited in both clearings at 8 and 15 m; *Pterygophora* and *Laminaria* recruited only in one clearing each at 21 m; and *Laminaria* also recruited in one clearing at 23 m. There was also much spatial variability in the recruitment of *Macrocystis* in deeper water; recruitment occurred in only one clearing at each of the 21- and 23-m sites. Even though *Macrocystis* recruited in only one clearing at 23 m, 12 *Eisenia* were tagged and monitored in the clearing with no *Macrocystis* to obtain more life history data for this species.

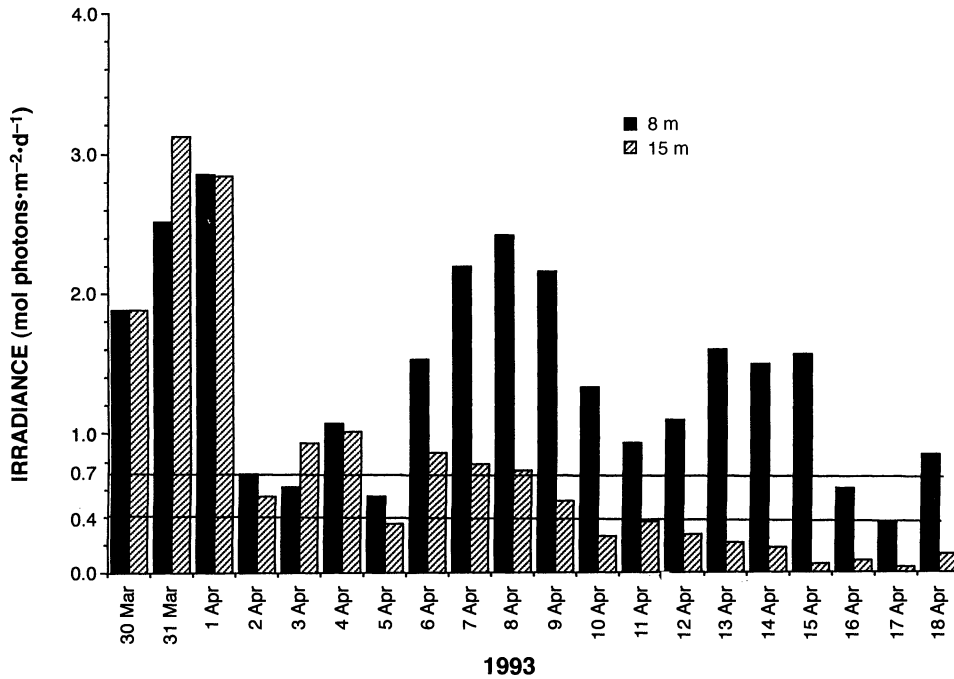


FIG. 4. Total daily irradiance measured on the bottom at two clearing sites in the Point Loma kelp forest, 30 March–18 April 1993. Measurements were made in areas with no *Macrocytis* canopy. The irradiance level of $0.4 \text{ mol photons} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ represents the lower limit of irradiance needed for *Macrocytis* gametogenesis to occur under ideal conditions. The irradiance level of $0.7 \text{ mol photons} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ represents the lower limit of irradiance needed for growth of *Macrocytis* sporophytes (Deysher and Dean 1984).

Macrocytis growth and reproduction.—To measure growth, we recorded the number of stipes per plant at a height of 1 m above the substratum, and holdfast volume was calculated from in situ measurements of height and two basal diameters, assuming the shape to be an elliptical cone (Ghelardi 1971). The volume of the bundle of sporophyll blades at the base of each plant was determined, assuming a cylinder from in situ measurements of height and diameter of the bundle. This is an indirect measure of reproductive effort, but Reed (1987) has shown that sporophyll biomass is closely related to zoospore production. We ranked the reproductive state for each plant on the following scale:

- 0) No sporophylls present.
- 1) Sporophylls present but no sorus development.
- 2) Sporophylls with sori only at the base of sporophylls.
- 3) Sporophylls with sori over most of the sporophylls surface.
- 4) Sporophylls with sori over all of the sporophylls surface.
- 5) Sporophylls with sori over all of the sporophylls surface releasing zoospores.

Growth and reproduction of understory kelps.—*Pterygophora* and *Laminaria* in the clearings were individually tagged at the same time as *Macrocytis*. *Eisenia* recruited and were tagged later. Growth of *Pterygophora* was determined by the method of DeWreede (1984). A 6-mm hole was punched in the midrib of the

terminal blade 30 mm from the base of the blade, and every 3 mo another hole was punched at the same location; the distance between the two holes was the linear growth of the blade. Reproductive effort for *Pterygophora* was evaluated by counting the number of sporophyll blades and sori per plant. *Eisenia* growth was evaluated by measuring stipe length, and reproductive capacity was evaluated by the number of sporophyll blades and sori. Growth of *Laminaria* was determined in a similar manner to *Pterygophora*. A 10-mm hole was punched 85 mm from the base of the blade and repunched in the same place every 3 mo; the distance between the two holes was the linear growth of the blade. Reproductive potential of *Laminaria* was evaluated as the percent of each blade covered by sori.

Reproduction of control kelps

To compare the reproductive output of understory species in our clearings with unmanipulated populations at 8, 15, and 21 m, each month from fall 1989–December 1991, we collected 25 *Pterygophora* and *Laminaria* from just outside our clearings. Plants were sampled haphazardly from areas with moderate *Macrocytis* densities. We recorded the number of *Pterygophora* sporophyll blades and sporophyll blades with sori, as well as the wet weight of the soral tissue and the wet weight of all sporophyll tissue. We also estimated the percent of *Laminaria* blades covered by soral tissue and calculated a reproductive index from the wet

weight of the stipe tissue divided by the total wet weight of the blade.

Module manipulations

Pterygophora.—To further assess the effects of inter- and intraspecific competition on growth and reproduction, we manipulated *Pterygophora* densities on modules. Recruits from margins of the 15-m clearing were attached to 30 × 30 cm polystyrene cube louver light diffusers (our modules). Individual *Pterygophora* holdfasts were threaded into three strand nylon lines that were attached to the modules with cable ties. These modules were cable-tied to spikes on the bottom, in the 8-, 15-, and 21-m sites. This allowed the modules to be brought to the boat for measurements of growth and reproduction, and then returned to their exact location. Ten modules with five plants and 10 modules with 25 plants were installed in each clearing. Five replicates of each *Pterygophora* density were installed in the high- and low-*Macrocystis* density treatments at each depth in 1989.

Eisenia.—In August 1989, 72 unbifurcated *Eisenia* were collected at the 15-m site and attached to 18 modules, each with four *Eisenia*. Thirteen *Eisenia* of the same age class and size were tagged and left attached to the natural substratum as controls. The modules were attached to stakes, in each half of each clearing, at 8, 15, and 21 m, with three replicates per treatment at each depth. Stipe length and bifurcation, and reproductive status were recorded quarterly over the next 2 yr.

Data analysis

We utilized generalized linear modeling (GzLM; McCullagh and Nelder 1989), as contained in SAS/Insight (1993), to determine the relative importance of various biological factors influencing kelp survivorship, abundance, growth, and reproduction. This method of analysis increases the flexibility and generality of the evaluation of data, particularly where nonnormal errors occur (Schneider 1994). Since many kinds of ecological data have nonnormal distribution of errors, GzLM is very useful by allowing specification of a variety of different error distributions: Poisson, binomial, and gamma distributions. The decision to use a particular model was made in an attempt to minimize error deviance and thus increase the "goodness of fit." Inspection of the error distribution of various data sets indicated a multiplicative increase of the error variance with the mean, so a gamma model with a log-link function was chosen for most analyses (Crawley 1993, Schneider 1994). We were interested in the response to treatment of each individual tagged plant, and this is the focus of the analysis. Separate analyses were performed on data from the two clearing experiments (initial years 1988 and 1993) at each depth. Data from same-depth clearings in the 1993 experiment were also analyzed separately to examine small spatial scale dif-

ferences. Each model was made up of growth, reproduction, density, or survivorship data as the response variable and *Macrocystis* stipe density as the independent variable. To examine the relative importance of inter- and intraspecific competition of the understory, *Pterygophora* density was also used as an independent variable, when appropriate.

We derived the most parsimonious model, following Occam's Razor, by using backwards selection (Crawley 1993) with an exit level of $\alpha < 0.10$. That is, we ran each model for analyses including both *Macrocystis* stipe density and *Pterygophora* density. Upon inspection of the level of significance (P) for each variable, the least significant variable was discarded and the resulting deviance checked. If the change in deviance was nonsignificant, then the term was permanently dropped from the model. In the tables, we present the P values, degrees of freedom, and the regression coefficients, to enable the reader to evaluate the relationships. Discarded variables are presented in the tables as nonsignificant (NS) with no regression coefficient.

It is important to note that the clearing experiments represent experimental treatments of high (ambient), low (one-third ambient), and zero *Macrocystis* plant densities across the depth gradient. The treatments were maintained by continually manipulating *Macrocystis* densities, and the results are presented in those terms. Due to the life history characteristics of this kelp, however, it appears that stipe density is the more sensitive indicator of the competitive effects of *Macrocystis* (Tegner et al. 1996, 1997). Generally, there is an inverse relationship between *Macrocystis* plant density and the average number of stipes per plant (North 1994). As a cohort undergoes self-thinning, stipe density remains relatively constant and appears to be a good indicator of environmental carrying capacity (Dayton et al. 1992, Tegner et al. 1996). While it was not practical to manipulate stipe density in these experiments, the data were collected, and we used this more appropriate variable in the actual statistical analyses. That is, the data presented in the tables utilize the more appropriate stipe density as an independent variable.

Different response variables had to be analyzed in different ways:

- 1) To compare response variables in both experiments (1988 vs. 1993) at comparable life history stages, a point in time near the termination of the shorter 1993 experiment (10 mo) was chosen for data to be analyzed along with the corresponding 10-mo time span in the 1988 experiment. To determine whether patterns apparent at this time persisted, data were again analyzed at the 25-mo point in the longer running 1988 experiment. *Macrocystis* stipes per plant, holdfast size, sporophyll condition, and algal densities were all analyzed in this manner.

- 2) Kelp survivorship was analyzed in terms of the number of weeks that individual tagged plants lived.

3) *Pterygophora* and *Laminaria* growth and reproduction data collected at the peak of the first growth and reproductive cycles were used because of strong seasonality of these variables.

4) Unfortunately, *Pterygophora* modules in one treatment at 8 m disappeared after 7 mo. The number of sporophyll blades per plant was analyzed at this last time point so that all treatments could be compared; trends were clearly apparent at this time.

We realize that comparison-wise error may increase when a large number of statistical tests are performed. Corrections of the α level reduce the probability of making a Type I error (i.e., accepting the existence of an effect that is not real), but also they increase the chance of making a Type II error (i.e., rejecting the existence of a real interaction). We consider the latter Type II error a more important risk. The experiments and comparisons reported here were logistically difficult and fraught with countless real world problems, common to diving research, that encompass important scales in space and time. That is, such a high energy and extremely variable coastal habitat imposes a great deal of natural variation into such experiments. Considering the amount of noise in the system, we adopted probabilities of $P = 0.10$ as sufficient evidence to imply a meaningful relationship. Most values were much more significant, and we simply present the uncorrected probabilities and the degrees of freedom, and allow readers to decide where they wish to be conservative. This approach of considering the weight of evidence, rather than testing point hypotheses, is in line with current thinking (McCullagh and Nelder, 1989, Brown 1995, McArdle 1996, Hilborn and Mangel 1997).

Data collected through the course of these experiments, which are presented as summary statistics in the tables, are also graphically presented in the Appendix, so that readers can evaluate depth-specific patterns of response and variation. Again, the actual experiments were analyzed with *Macrocystis* stipe densities as the treatment variable, rather than plant densities. Plant densities, however, are presented in the figures and were what we actually manipulated.

RESULTS

Physical environment

The study period (1988–1995) was marked by strongly varying temperature regimes (Fig. 2). During the 1988–1989 La Niña event, bottom temperatures were predominantly $<14^{\circ}\text{C}$, the isotherm indicating water with adequate nutrients, and were above the 16°C threshold for nitrate detection for a negligible period of time. Strong but intermittent El Niño conditions persisted during 1992 and 1993 (Hayward 1993, Hayward et al. 1994), and bottom temperatures were $>16^{\circ}\text{C}$ for much of these years (Fig. 2B). Stratification of the water column is reduced during strong El Niño events as the 14°C isotherm is depressed below kelp forest depths

(Tegner and Dayton 1987). During 1994, circulation returned to non-El Niño conditions, but sea surface and bottom temperatures were again anomalously warm during most of the year, as well as in the first quarter of 1995 (Hayward et al. 1995). While surface temperatures in 1992–1994 reached levels comparable with the 1982–1984 El Niño, the strong spring upwelling observed during 1991, 1992 (Tegner et al. 1995), 1993, and 1994 sharply contrasts recent temperature regimes with the massive earlier El Niño. For purposes of brevity, we will call the 1988–1992 experiments the La Niña set, and the 1993–1995 experiments the El Niño set.

To better understand physical gradients, these experiments were conducted at shallower and deeper sites than our previously published temperature data (Dayton et al. 1992, Tegner et al. 1996). The temperature records from 8 and 21 m generally follow the same seasonal patterns as 12, 15, and 18 m; differences among sites are maximal in the spring and summer, decrease during the fall, and virtually disappear during winter (Fig. 2). The pattern of significantly cooler temperatures with increasing depth holds for these additional sites as well; 8 m is significantly warmer than 12 m (paired t test, $P < 0.005$), although temperatures from the two sites are highly correlated (simple linear regression, $r^2 = 0.7$). Despite its shallow depth, the temperature pattern at 8 m is closer to that of the rest of the kelp forest than the sea surface, from which it is also significantly different ($P < 0.005$, $r^2 = 0.5$). This is supported by higher frequency observations (samples every 10 min) of surface and bottom temperatures at the 8-m site, which show much larger amplitude tidal variations on the bottom than on the surface (*unpublished data*). Similarly, 21 and 23 m (for which we do not have overlapping data) are both significantly colder than 18 m ($P = 0.001$, $r^2 = 0.93$; $P < 0.001$, $r^2 = 0.95$, respectively).

Total daily irradiance in high- and low-*Macrocystis* treatments at 8, 15, and 21 m from December 1989–December 1991 is presented in Fig. 3. Despite the many periods for which there are no data, marked relationships between irradiance and depth and canopy cover are obvious. Fig. 4 presents total daily irradiance data collected in March and April 1993 at the 8- and 15-m sites. Note that the 8-m low-canopy treatments had much more light in 1990 and 1991 than did the adjacent no-canopy treatment in 1993, reflecting the lack of light penetrating the plankton blooms that pervaded the kelp forest during that time. Irradiance levels of $0.4 \text{ mol photons}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and $0.7 \text{ mol photons}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ represent the lower limits of irradiance needed for gametogenesis and growth of *Macrocystis* sporophytes under ideal temperature and nutrient stress conditions. A minimum of 10 continuous days with irradiance at $\geq 0.4 \text{ mol photons}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ is necessary for gametogenesis. At lower irradiance, gametophytes take longer to produce sporophytes, with a corresponding risk of increased mortality (Deysher and Dean 1984, 1986). Fig. 4 suggests

that benthic light levels, especially at 15 m, limited recruitment during the observation period. Total daily irradiance levels at these two sites demonstrate the poor water conditions for light transmission noted for much of spring 1993.

Finally, we evaluated the actual effect of high- and low-*Macrocystis* densities on irradiance levels by assuming the relative irradiance at the maximum recording station, "8 m low," as 1.00 and calculating monthly ratios of 8 m low density to the other irradiance stations. These monthly ratios were averaged between December 1989 and August 1991. The mean values were: 8 m low = 1.00; 8 m high = 0.35; 15 m low = 0.22; 15 m high = 0.10; and 21 m low = 0.04. These data (Fig. 3) show the substantial differences with both depth and experimental thinning of giant kelp density.

Kelp recruitment: background patterns of populations of Macrocystis, Pterygophora, and Laminaria

Macrocystis recruitment events of 1988–1989 and 1993–1994 on the permanent transects differed in magnitude (Tegner et al. 1996, 1997), and these distinctions were also seen in the patterns of plant and stipe densities in our experimental clearings (Figs. 5 and 6). The contrasts probably reflect the divergent storm patterns (e.g., Reed et al. 1988) during these periods, as well as reflecting the strong *Macrocystis* canopy suppression of the understory during the La Niña and poor water visibility in spring 1993. During spring–early summer 1988, water temperatures were cool. Also, because of the massive storm, the canopy was negligible and there was much more light than in 1993. This resulted in heavy 1988 recruitment of all kelps along the transects at 18-, 15-, and 12-m depths (Tegner et al. 1996, 1997). Bottom temperatures in 1993 were $\sim 1^\circ\text{C}$ higher than those in 1988 (Fig. 2), and *Macrocystis* recruitment was much slower and less intense, in contrast with the massive event in 1988.

Tegner et al. (1996, 1997) demonstrated that differences in *Macrocystis* stipe densities between the 1988 and 1993 cohorts apparently had strong effects on the success and distribution of understory species, and this related to the importance of oceanographic climate events on *Macrocystis* stipe density and canopy cover, with subsequent cascading effects on the abundance of the understory. Density and reproductive condition of the two most important understory species, *Pterygophora* and *Laminaria*, are offered in Figs. 7–9. Here we extend these data with actual experiments designed to identify thresholds. The reference data for *Pterygophora* reproduction (Fig. 8) show a winter peak for both percentage of plants with soral tissue and reproductive index (McPeak 1981), with a much higher proportion being reproductive in shallower depths. While there is more noise, much the same pattern was observed for *Laminaria* (Fig. 9). However, again note that La Niña stimulation of the *Macrocystis* canopy (Tegner

et al. 1996, 1997) may be responsible for much lower reproductive indices before late 1990.

Canopy-thinning and clearance experiments:

I. Macrocystis on Macrocystis

Plant and stipe density.—The *Macrocystis* manipulation involved the removal of all nonencrusting macroalgae, allowing natural recruitment. The density of giant kelp then was manipulated and new recruits thereafter were removed. Relative experimental densities were maintained after quarterly assessments of 120 m²/treatment. The differences between the La Niña and El Niño experiments were dramatic, as *Macrocystis* densities varied over an order of magnitude, and there were strong depth-related density differences in both cohorts (Fig. 5).

We were able to manipulate the density of giant kelp plants, but stipe density most closely reflects the amount of light interference that *Macrocystis* exerts on the understory. While not directly manipulated, stipe densities were quantified (Fig. 6), and the densities following the initial clearings in 1988 dropped from levels of 310/m² at 8 m, 200/m² at 15 m, and 50–100/m² at 21 m to relatively low levels that then remained rather steady for the following 2 yr. However, instead of a steep decline from initial densities in 1993, the pattern was one of an increase in stipe density at all depths for the first year. In fact, there was no *Macrocystis* recruitment at 21 m until January 1994, 10 mo after that clearing was completed. Recruitment at one of the two clearings was sparse, and the small sporophytes were completely grazed away, as a front of sea urchins moved through. At 23 m, recruitment was not evident until June 1994, 14 mo after that clearing was initiated, and then in only one of the two clearings. Because *Macrocystis* recruits were removed after initial densities were established in the experimental areas, the effect of stipe density on *Macrocystis* recruitment could not be evaluated.

Survivorship.—The effect of *Macrocystis* intraspecific competition should be evident as survivorship at three depths in low- and high-density treatments during the poststorm 1988–1989 La Niña and 1992–1994 El Niño conditions. In the 1988–1989 experiment, low density treatments tended to have higher survivorship, but there was no significant intraspecific difference between the treatments (Table 1; Fig. A1 in the Appendix). In the 1993 experiment there were consistent effects of depth on survivorship, with the shallow 8-m plants suffering high initial mortality (probably reflecting the relatively high initial density); the 15-m plants had intermediate mortality, and the deep 21- and 23-m plants had relatively low recruitment and high survivorship. However, only one of the shallow 8-m clearings had a significant negative intraspecific effect; the other showed no difference between treatments. This lack of significance probably relates to small-scale (10–100 m²) patchiness in recruitment.

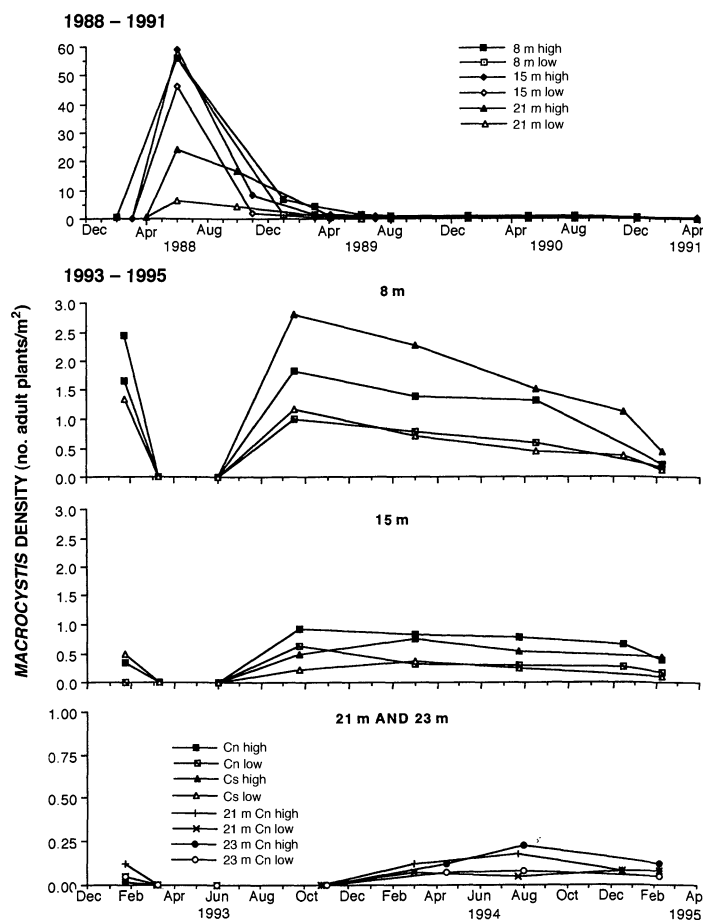


FIG. 5. Density of *Macrocystis* in the clearing experiments of 1988–1991 and 1993–1995, in the Point Loma kelp forest. The data from the high- and low-density *Macrocystis* treatments of the 1988–1991 experiment, and from the two clearings (Cn, north clearing; Cs, south clearing) of the 1993–1995 experiment, are plotted. Note the change in scale among the graphs. Densities prior to clearing are plotted in the 1993–1995 graphs.

Growth.—The number of stipes on each *Macrocystis* plant 1 m above the substratum showed similar trends in both experiments, although the La Niña conditions seemed to support more stipes overall and had greater variation between depths and densities (Fig. A2 in the Appendix). With regard to the intraspecific effects of stipe density on number of new stipes per plant in 1988, after 10 mo there were very strong negative relationships at 8 and 15 m, and an important relationship at 21 m (Table 2); this pattern of significant differences at 8 and 15 m continued to 25 mo. Again, in contrast to the La Niña, there was no hint of an intraspecific effect of stipe density on stipes per plant in the El Niño experiment (Table 2).

***Macrocystis* holdfasts** (Fig. A3 in the Appendix) obtained larger size at all depths and again had greater variation among depths during the La Niña. Clearly higher nutrients enhanced growth of both the canopy and the holdfasts. Because holdfast size probably integrates more physiological factors involved with the health of the plant, this may be a more conservative measure of environmental conditions than stipe numbers. During the nutrient-rich La Niña, there were very strong treatment effects, with *Macrocystis* stipe density negatively affecting holdfast size (Table 2) after 10 and

25 mo. This negative relationship persisted, but was much less significant during the El Niño; at the 8 m south site there was a positive relationship, but not at 8 m north. Both 15-m sites were significant. The 21 m north site did not have a significant relationship, and the 23 m north site had a negative relationship. Thus, again, the strong interactions were associated with nutrient-rich conditions of La Niña, and this pattern broke down during the 1993 El Niño, which even had positive relationships.

Reproduction.—Growth of sporophylls represents an important evolutionary adaptation to disturbance and environmental change. Reed et al. (1996) discussed the relationship between reproductive responses and resources, and Reed (1987) reported a strong relationship between biomass and zoospore production; because our treatments induced differences in growth, we hypothesized that there should also be differences in reproduction. Two reproductive indicators were evaluated: (1) sporophyll bundle volume (Fig. A4 in the Appendix), and (2) sporophyll condition (Fig. A5 in the Appendix), assessed on a scale of 0–5, in which 0 = no sporophylls present, and 5 = sporophylls actually releasing zoospores (Table 2).

The volume of sporophyll bundles during the La

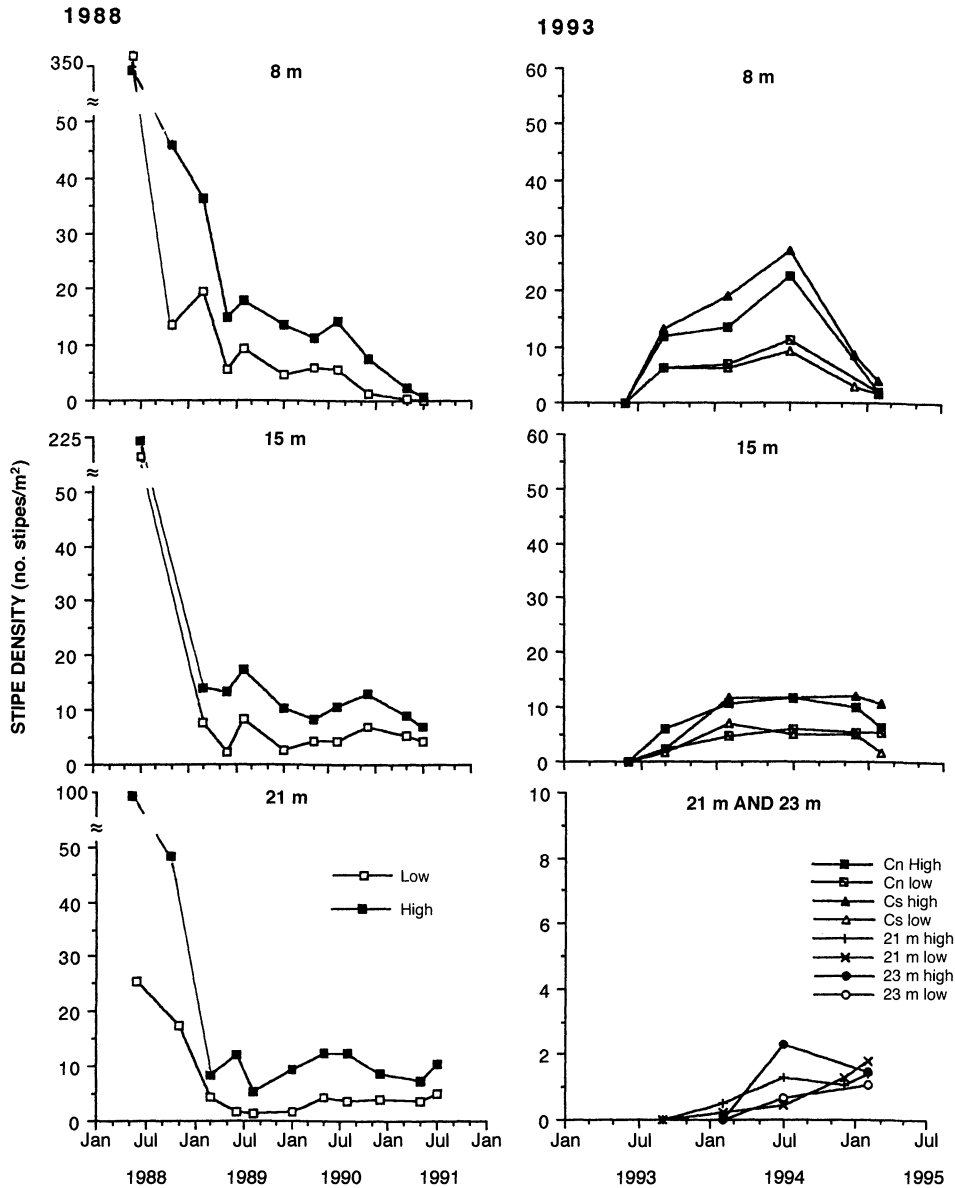


FIG. 6. *Macrocystis* stipe density (no. stipes/m²) in the clearing experiments of 1988–1991 and 1993–1995. The data from the high- and low-density *Macrocystis* treatments of the 1988–1991 experiment and from both clearings (Cn, north clearing; Cs, south clearing) of the 1993–1995 experiment are plotted. Note the change in scale among the graphs.

Niña was larger than the El Niño years (Fig. A4 in the Appendix). After 10 and 25 mo, sporophyll bundle size was highly significantly negatively influenced by stipe density during the La Niña (Table 2). However, the only negative relationships between sporophyll bundle size and stipe density during the El Niño were at 15 m, both north and south. This is strong evidence of an interaction between nutrient availability and density dependent reproduction. In fact, in the first experiment, sporophyll bundles at 21 m were larger than those in shallow water. This suggests that the size of the bundles is heavily influenced by nutrients, as this area of the

kelp forest consistently had colder, presumably more nutrient-rich waters.

Sporophyll reproductive condition data (Fig. A5 in the Appendix) follow similar patterns as those of bundle volume. There were negative density effects among treatments after 10 mo at 8, 15, and 21 m during the La Niña (Table 2). After 25 mo, these effects were largely lost as only 15 m had a negative effect. In the El Niño experiment, there was only one negative effect at the 23 m north site. The appearance of the first sori at the shallower sites was much faster under La Niña conditions than in the El Niño experiment: 1.5 vs. 5.5

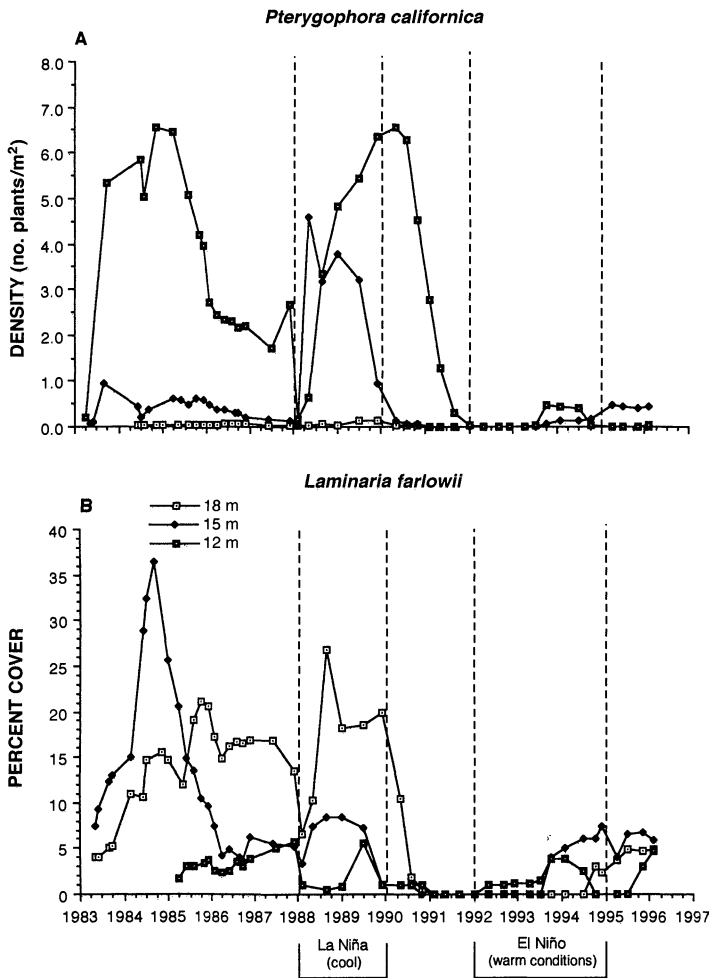


FIG. 7. (A) Density of *Pterygophora* and (B) percent cover of *Laminaria* along transect lines at three sites in the Point Loma kelp forest, 1983–1996. Modified from Tegner et al. (1997).

mo at 8 m, and 2.5 vs. 6.0 mo at 15 m. Plants at 21 m did not become reproductive until 10–13.5 mo after the experiment started, whereas 21- and 23-m plants became reproductive in 6–9 mo in 1993.

Canopy-thinning and clearance experiments: *II. Macrocystis and/or Pterygophora effects on* *Pterygophora*

Density.—*Pterygophora* responded to major disturbances, such as the 1982–1984 ENSO and the 1988 storm (Dayton et al. 1992), on both the transect lines (Fig. 7) and in the experimental plots (Fig. A6 in the Appendix). The background densities observed along the transect lines showed relatively high shallow water recruitment with densities of 6–7 plants/m², while the deeper sites were <1 plant/m². The 1988 storm cleared much of the substratum, vastly reducing the density of all algae, and there was massive *Pterygophora* recruitment of 100–200 plants/m². This soon decreased considerably, as the strong La Niña *Macrocystis* competition took effect (Tegner et al. 1997), and the background densities were very much lower during the 1993 El Niño than during the La Niña conditions of the late

1980s. After 10 mo during the La Niña, *Macrocystis* had strong negative effects at 8 m and a strong positive effect at 15 m (Table 3). Furthermore, probably because densities were very low, the same sites after 25 mo had negative effects. Densities at 21 m were very low, and there was never an effect at 21 m during the La Niña. For some reason, the 15-m site had stronger recruitment in 1993 than did the 8-m site. While the densities at 21 m during the 1992–1993 El Niño were very much lower than at shallower depths, they began to increase at about the same time that densities decreased at 15 m. In 1993 the densities remained virtually unchanged at 8 and 15 m. There was only one significant effect of *Macrocystis* stipe density on *Pterygophora* density at the 8 m south site (Table 3).

Survivorship.—Table 1 summarizes the interspecific effects of *Macrocystis* density on *Pterygophora* survivorship (Fig. A7 in the Appendix). *Pterygophora* survivorship was very similar at both depths and treatments in 1988. The 1993 experiment was extremely variable, yet there was a highly significant negative *Macrocystis* effect on *Pterygophora* survivorship at 8

FIG. 8. Percentage of 25 *Pterygophora*, which were collected every month during March 1990–December 1991, that were reproductive, and the mean reproductive index ($[(\text{sorus wet mass})/(\text{total sporophyll wet mass})] \times 100$). *Pterygophora* were collected from areas with moderate *Macrocystis* canopy near the clearing sites at 8, 15, and 21 m in the center of the kelp forest.

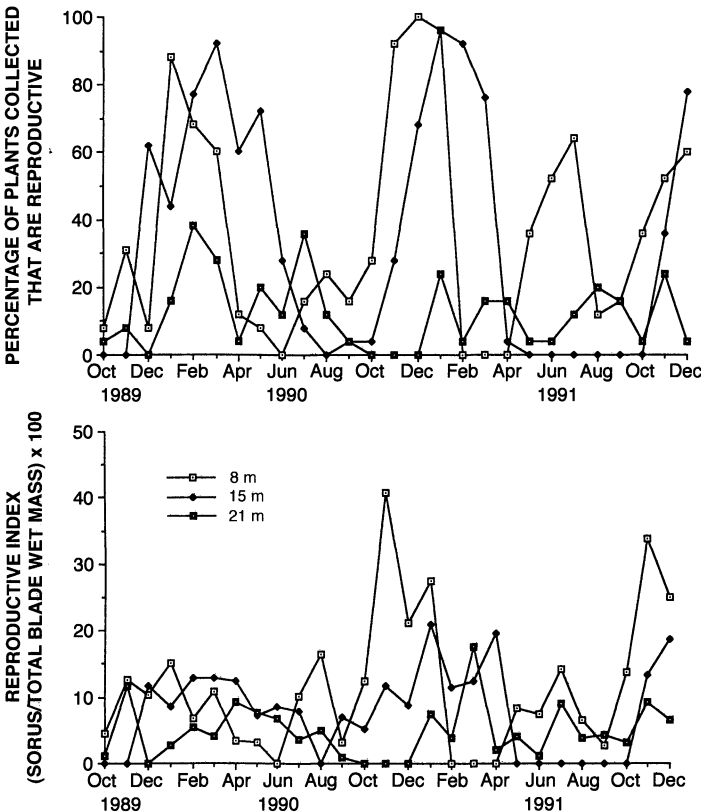
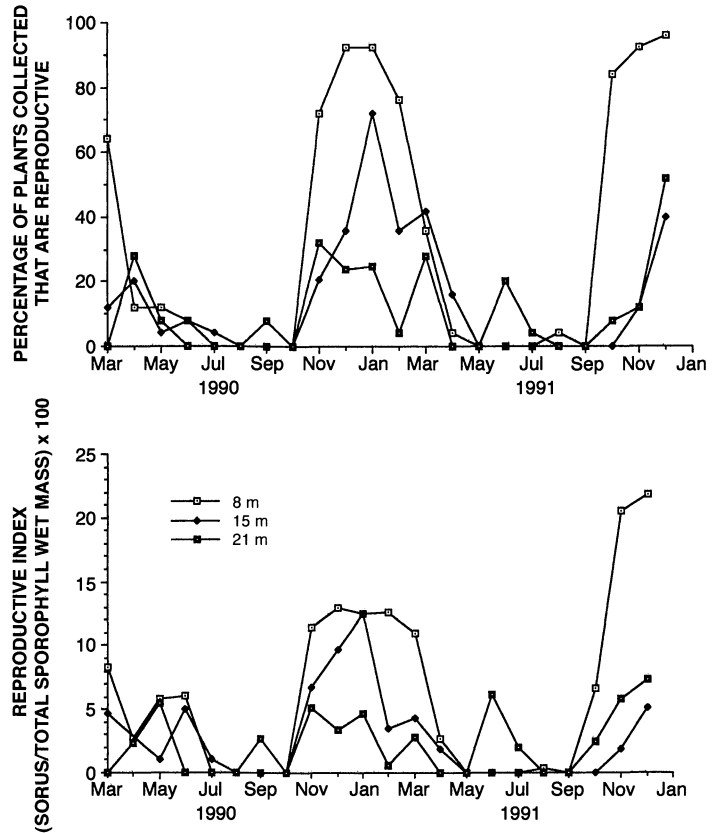


FIG. 9. Percentage of 25 *Laminaria*, which were collected every month during March 1990–December 1991, that were reproductive, and the mean reproductive index ($[(\text{mean sorus wet mass})/(\text{total blade wet mass})] \times 100$). *Laminaria* were collected from areas with moderate *Macrocystis* canopy near the clearing sites at 8, 15, and 21 m in the center of the kelp forest.

TABLE 1. Summary of the analyses of the effects of *Macrocystis* stipe density on the survivorship of tagged plants using Generalized Linear Modeling. The number of months that each plant survived was used as the dependent variable.

Species	Initial year	Depth (m)	<i>Macrocystis</i> effect		
			Error (df)	Probability (P)	Regression coefficient
<i>Macrocystis</i>	1988	8	37	NS	...
		15	30	NS	...
		21	18	NS	...
	1993	8 south	29	0.0121	-0.39
		8 north	29	NS	...
		15 south	29	NS	...
		15 north	29	NS	...
		21 south
		21 north	26	NS	...
		23 south
		23 north	20	NS	...
<i>Pterygophora</i>	1988	8	48	NS	...
		15	49	0.0276	-0.45
		21	...	No tagged plants	...
	1993	8 south	44	NS	...
		8 north	44	0.0001	-0.69
		15 south	44	NS	...
		15 north	44	NS	...
		21 south
		21 north	32	NS	...
		23 south
		23 north	...	No tagged plants	...
<i>Laminaria</i>	1988	8	28	0.0001	-1.21
		15	30	0.0001	-0.97
		21	29	NS	...
	1993	8 south	41	NS	...
		8 north	43	NS	...
		15 south	44	0.0580	-0.19
		15 north	44	NS	...
		21 south
		21 north	44	NS	...
		23 south
		23 north	44	NS	...

Notes: Separate analyses were performed on data from each clearing at each depth. The P value of the effect of the independent variable, *Macrocystis* stipe density, is presented if <0.10; NS = not significant.

m north; all of the rest of the comparisons were insignificant.

Growth.—Terminal blade growth of *Pterygophora* (Fig. A8 in the Appendix) was seasonal and very strongly affected by the *Macrocystis* density treatment in 1988, at both 8 m and 15 m (Table 3). In 1993 there were negative effects of *Macrocystis* stipe density at both the 8- and 15-m sites, but not at 21 or 23 m. Clearly *Macrocystis* can have a very powerful effect on *Pterygophora* growth, apparently much stronger than the depth effect.

Reproduction.—The number of sporophylls per *Pterygophora* plant was similar during the La Niña and El Niño periods, except that the deep 21-m plants did not become reproductive in 1993 (Fig. A9 in the Appendix). It is interesting to note that the single 8 m low-density plant surviving through 1991 had many more fertile sporophylls than the other plants. During the 1988 La Niña, *Macrocystis* stipe density negatively impacted *Pterygophora* sporophyll production at 8 m and 15 m (Table 3). In the 1993 experiment, there were negative effects of *Macrocystis* stipe density on spo-

rophyll production at all sites. Clearly, *Macrocystis* has very strong interspecific effects on *Pterygophora* sporophyll production. There is no evidence that *Pterygophora* are deciduous at Point Loma, as has been reported for more northerly populations (Reed 1987).

The effects of *Macrocystis* stipe density on the production of sori on *Pterygophora* sporophyll blades were highly variable, although the seasonality noted by Reed et al. (1996) was apparent, especially under El Niño conditions (Fig. A10 in the Appendix). In 1989, the percentage of sporophyll blades per plant that were reproductive may have been relatively high, but, since monitoring was not performed until late spring, the peak was not recorded. During the second spring, few blades became reproductive. This pattern differed in the 1993–1995 experiment; in 1994, the percentage of reproductive blades was relatively low, at 8 and 15 m, compared with soral production during the plants' third spring. The negative effects of *Macrocystis* stipe density varied from not significant at 8 m south and 15 m north to highly significant at 8 m north and at 15 m south (Table 3). Because *Pterygophora* recruited in

TABLE 2. Summary of the analyses of the intraspecific effects of *Macrocystis* stipe density on stipes per plant, holdfast volume, sporophyll bundle volume, and sporophyll condition using Generalized Linear Modeling.

Response variable	Initial year	Depth (m)	<i>Macrocystis</i> effect					
			After 10 mo			After 25 mo		
			Error (df)	Probability (P)	Regression coefficient	Error (df)	Probability (P)	Regression coefficient
Stipes per plant	1988	8	25	0.0004	-0.07	24	0.0448	-0.03
		15	27	0.0001	-0.05	23	0.0001	-0.13
		21	19	0.0535	-0.04	19	NS	
	1993	8 south	19	NS				
		8 north	23	NS				
		15 south	21	NS				
		15 north	17	NS				
		21 south				
		21 north	13	NS				
		23 south				
		23 north	13	NS				
Holdfast volume	1988	8	25	0.0001	-0.14	24	0.0004	-0.05
		15	27	0.0001	-0.14	23	0.0001	-0.12
		21	19	0.0001	-0.11	19	0.0026	-0.06
	1993	8 south	19	0.0096	-0.03			
		8 north	23	NS				
		15 south	21	0.0879	+0.06			
		15 north	17	0.0481	-0.11			
		21 south				
		21 north	13	NS				
		23 south				
		23 north	13	0.0801	-1.95			
Sporophyll bundle volume	1988	8	25	0.0001	-0.21	24	0.0047	-0.10
		15	27	0.0001	-0.22	23	0.0001	-0.20
		21	19	0.0001	-0.15	19	0.0104	-0.13
	1993	8 south	19	NS				
		8 north	23	NS				
		15 south	21	0.0391	-0.07			
		15 north	17	0.0536	-0.12			
		21 south				
		21 north	13	NS				
		23 south				
		23 north	13	NS				
Sporophyll condition	1988	8	25	0.0041	-0.07	24	NS	
		15	27	0.0156	-0.04	23	0.0164	-0.11
		21	19	0.0030	-0.07	19	NS	
	1993	8 south	19	NS				
		8 north	23	NS				
		15 south	21	NS				
		15 north	17	NS				
		21 south				
		21 north	13	NS				
		23 south				
		23 north	13	0.0005	-3.42			

Notes: Separate analyses were performed on data from each clearing at each depth at 10 and 25 mo. The *P* value for the effect of the independent variable, *Macrocystis* stipe density, is presented if <0.10; NS = not significant. No data are available for empty blocks in the table.

mid-1994 at 21 m, data are only from 1995. This temporal variation may reflect release from the El Niño and improved temperature/nutrient conditions. Statistical analysis was not performed on the data from the first experiment, because there was no concurrent peak in reproduction of plants from the treatments. *Pterygophora* in the 1988 experiment required 12–16.5 mo for appearance of the first sori (except 8 m high which never became reproductive), but under El Niño conditions, most sites developed initial sori within 5–11 mo (8 m high required 20 mo).

Intraspecific Pterygophora effects on growth and reproduction.—Reed (1990) attributed intraspecific density dependence in *Pterygophora* growth and reproduction to competition for light. Probably reflecting the extremely high densities, we also found very strong intraspecific *negative* effects of *Pterygophora* density on growth at both 8 and 15 m in 1989 (Table 3). We found, however, very strong intraspecific *positive* effects of *Pterygophora* density on growth at 8 m south in 1993 (Table 3). One explanation might be that there was a high *Pterygophora* density under a low *Mac-*

TABLE 3. Summary of the analyses of the interspecific effects of *Macrocystis* stipe density on *Pterygophora* density, growth, sporophyll production, and reproductive effort using Generalized Linear Modeling. Intraspecific effects were examined by using *Pterygophora* density as a second independent variable in the analysis of growth, sporophyll blades, and reproductive effort.

Response variable	Initial year	Depth (m)	Error (df)	After 10 mo				After 25 mo				
				<i>Macrocystis</i> effect		<i>Pterygophora</i> effect		Error (df)	<i>Macrocystis</i> effect		<i>Pterygophora</i> effect	
				Probability (P)	Regression coefficient	Probability (P)	Regression coefficient		Probability (P)	Regression coefficient	Probability (P)	Regression coefficient
Density	1988	8	4	0.0001	−0.09			4	0.0050	−0.16		
		15	4	0.0131	+0.07			4	0.0623	−0.28		
		21	4	NS				4	NS			
	1993	8 south	7	0.0714	−0.04							
		8 north	7	NS								
		15 south	7	NS								
		15 north	7	NS								
		21 south								
		21 north	7	NS								
		23 south								
23 north		7	NS									
Growth rate (mm/day)	1988	8	25	0.0001	−0.17	0.0001	−0.16		(100% mortality in high <i>Macrocystis</i> by 25 mo)			
		15	28	0.0001	−0.19	0.0001	−0.18		(100% mortality in high <i>Macrocystis</i> by 25 mo)			
		21	†									
	1993	8 south	5	0.0294	−0.03	0.0116	+0.33					
		8 north	32	0.0001	−0.08	NS						
		15 south	11	0.0001	−0.11	NS						
		15 north	36	0.0002	−0.07	NS						
		21 south	...									
		21 north	‡	...								
		23 south	...									
23 north		†										
Number of sporophyll blades per plant	1988	8	27	0.0001	−0.28	0.0001	+0.26		(100% mortality in high <i>Macrocystis</i> by 25 mo)			
		15	33	0.0001	−0.17	0.0001	−1.28		(100% mortality in high <i>Macrocystis</i> by 25 mo)			
		21	†									
	1993	8 south	36	0.0004	−0.02	NS						
		8 north	43	0.0001	−0.05	0.0139	−0.69					
		15 south	35	0.0001	−0.06	NS						
		15 north	43	0.0134	−0.03	NS						
		21 south	...									
		21 north	19	0.0430	+0.29	NS						
		23 south	...									
23 north		†										
Percentage of reproductive blades per plant	1988	8	§						(100% mortality in high <i>Macrocystis</i> by 25 mo)			
		15	§						(100% mortality in high <i>Macrocystis</i> by 25 mo)			
		21	§									
	1993	8 south	28	NS		0.0214	+0.65					
		8 north	33	0.0001	−0.14	NS						
		15 south	29	0.0017	−0.15	NS						
		15 north	32	NS		NS						
		21 south								
		21 north	18	NS		NS						
		23 south								
23 north		†										

Notes: Separate analyses were performed using data from each clearing at each depth at 10 and 25 mo. *P* values for the independent variables, *Macrocystis* stipe density and *Pterygophora* density, are presented if <0.10. NS = not significant. No data are available for empty blocks in the table.

† No tagged plants.
‡ No growth peak.
§ No seasonal peak.

TABLE 4. Summary of the analyses of the interspecific effects of *Macrocystis* stipe density and the intraspecific effects of *Pterygophora* density on *Pterygophora* growth, sporophyll blade production, and survivorship of *Pterygophora* on modules.

Response variable	Depth (m)	Error (df)	<i>Macrocystis</i> effect		<i>Pterygophora</i> effect	
			Probability (<i>P</i>)	Regression coefficient	Probability (<i>P</i>)	Regression coefficient
Growth	8	16	0.0001	-0.14	0.0054	-0.01
	15	17	0.0001	-0.15	NS	...
	21	17	0.0029	-0.10	NS	...
Number of sporophyll blades per plant	8	10	0.0001	-0.23	0.0567	-0.03
	15	9	0.0001†	-2.89	0.0001	-0.03
	21	12	NS	...	NS	...
Percentage of reproductive blades per plant	8	10	0.0001	-1.36	NS	...
	15	9	0.0001†	-2.89	NS	...
	21	12	NS	...	0.0001	+0.06
Survivorship	8	‡				
	15	16	0.0001	-0.25	NS	...
	21	16	NS	...	0.0180	-0.04

Notes: Separate analyses were performed on data from each clearing at each depth. *P* values for the effects of the independent variables, *Macrocystis* stipe density and *Pterygophora* density, are presented if <0.10; NS = not significant. For more details of the analysis of growth, see *Data analysis* section of text.

† Plants in high stipe density treatment had 0 sporophyll blades after 2 mo.

‡ Some modules lost.

Macrocystis canopy. Thus, there might have been release from *Macrocystis* competition expressed as a positive intraspecific *Pterygophora* relationship. At 15 m in 1988, we found the expected strong negative intraspecific *Pterygophora* relationship.

We also analyzed the intraspecific effects of *Pterygophora* density on *Pterygophora* sporophyll production (Table 3). During the 1988–1989 La Niña, there were highly significant effects at both 8 and 15 m, but the 8-m site had a positive relationship, whereas the 15-m site had a negative relationship. There were no tagged *Pterygophora* at 21 m during La Niña. At 8 m north during the 1993 El Niño, however, there was a negative effect of *Pterygophora* density on sporophyll production, but no other significant intraspecific effects on *Pterygophora* sporophyll number.

The spatial variability in soral production occurred not only with respect to the *Macrocystis* effect, but also with the intraspecific *Pterygophora* effects (Table 3). Soral production was strongly affected by *Macrocystis* density at 8 m north, but not at 8 m south, which actually had a strong positive *Pterygophora* density effect. There were no other negative *Pterygophora* effects. Again, this may be because the *Pterygophora* density was higher in low *Macrocystis* treatment, and *Pterygophora* were, therefore, much more fertile.

Pterygophora module experiments.—In 1989 we tested the effects of *Macrocystis* and *Pterygophora* on survivorship, growth, and reproduction of *Pterygophora* plants that were transplanted on modules (Fig. A11 in the Appendix). Three modules in one treatment were lost at 8 m, so testing of survivorship was not possible. There was a strong negative *Macrocystis* effect on survivorship (Table 4) at 15 m, but not at 21 m. In contrast and perhaps reflecting the lack of a *Macrocystis* effect

at 21 m, there was a strong negative intraspecific *Pterygophora* effect at 21 m. There was also a strong negative *Macrocystis* stipe effect on *Pterygophora* growth (Fig. A12 in the Appendix) at all three depths. The intraspecific negative effect of *Pterygophora* (as manipulated on the modules) on *Pterygophora* growth was significant only at 8 m. The lack of an intraspecific effect was probably due to the strong effect of *Macrocystis*.

The two shallow sites, 8 and 15 m, had strong negative *Macrocystis* effects on *Pterygophora* sporophyll production (Fig. A13 in the Appendix), but not the deeper 21-m site (Table 4). Interestingly, there were strong intraspecific effects of *Pterygophora* density on sporophyll production at 8 and 15 m. Finally, the mean percent of sporophylls per plant with sori (Fig. A14 in the Appendix) was significantly negatively affected by *Macrocystis* stipe density at 8 and 15 m, but not at 21 m. Again, possibly reflecting release from this strong *Macrocystis* canopy effect, there were no intraspecific *Pterygophora* effects at those depths but there was a very strong positive intraspecific effect at 21 m, where there had been no *Macrocystis* effects (Table 4).

Canopy-thinning and clearance experiments:

III. Effects of *Macrocystis* and/or *Pterygophora* on *Laminaria*

Density.—The effects of *Macrocystis* or *Pterygophora* overstories on *Laminaria* were variable (Fig. A15 in the Appendix). A recruitment peak at 15 m low density in 1989 was associated with a die-off of *Desmarestia*, which inhibits kelp recruitment (Dayton et al. 1992). Analyses of the 1988 experiments, after 10 mo (Table 5), show negative effects of *Macrocystis* stipe density on *Laminaria* density at 15 m, but not at

TABLE 5. Summary of the analyses of the interspecific effects of *Macrocystis* stipe density on *Laminaria* density, growth, and reproductive effort using Generalized Linear Modeling. Interspecific effects of *Pterygophora* density as a second independent variable in the analyses of density, growth, and reproductive effort.

Response variable	Initial year	Depth (m)	Error (df)	After 10 mo				After 25 mo				
				<i>Macrocystis</i> effect		<i>Pterygophora</i> effect		<i>Macrocystis</i> effect		<i>Pterygophora</i> effect		
				Probability (P)	Regression coefficient	Probability (P)	Regression coefficient	Probability (P)	Regression coefficient	Probability (P)	Regression coefficient	
Density	1988	8	4	NS	...	NS	...	4	0.0004	-0.52	NS	...
		15	4	0.0003	-0.51	NS	...	4	NS	...	NS	...
		21	4	NS	...	0.0253	+0.85	4	NS	...	NS	...
	1993	8 south	7	0.0208	-0.07	0.0001	+0.38					
		8 north	7	0.0001	-0.10	NS	...					
		15 south	7	NS	...	NS	...					
		15 north	7	0.0159	-0.10	NS	...					
		21 south					
		21 north	4	NS	...	NS	...					
		23 south					
		23 north	4	NS	...	NS	...					
Growth	1988	8	(100% mortality of tagged plants in high <i>Macrocystis</i>)				(100% mortality of tagged plants in high <i>Macrocystis</i>)					
		15	12	0.0001	-0.25	0.0001	+0.14	(100% mortality of tagged plants in high <i>Macrocystis</i>)				
		21	26	0.0001	-0.07	0.0001	-0.50	(100% mortality of tagged plants in high <i>Macrocystis</i>)				
	1993	8 south	19	0.0148	...	NS	...					
		8 north	36	0.0001	...	NS	...					
		15 south	15	0.0001	...	0.0001	-18.56					
		15 north	...	NS	...	NS	...					
		21 south					
		21 north	32	0.0103	-28.9	0.0117	-12.19					
		23 south					
		23 north	28	0.0009	-0.56	0.0015	+54.41					
Percentage of blade covered by sorus	1988	8	(100% mortality of tagged plants in high <i>Macrocystis</i>)				(100% mortality of tagged plants in high <i>Macrocystis</i>)					
		15	26	NS	...	NS	...	(100% mortality of tagged plants in high <i>Macrocystis</i>)				
		21	20	0.0001	-0.84	NS	...	(100% mortality of tagged plants in high <i>Macrocystis</i>)				
	1993	8 south	35	NS	...	0.0191	-0.67					
		8 north	42	NS	...	NS	...					
		15 south	35	NS	...	NS	...					
		15 north	34	NS	...	NS	...					
		21 south					
		21 north	(No <i>Laminaria</i> were reproductive)									
		23 south					
		23 north	42	NS	...	NS	...					

Notes: Separate analyses were performed on data from each clearing at each depth and for density data, at 10 and 25 mo. *P* values for the effects of the independent variables, *Macrocystis* stipe density and *Pterygophora* density, are presented if <0.10; NS = not significant. For more details of the analysis of growth, see *Data analysis* section of text. No data are available for empty blocks in the table.

8 or 21 m. It is interesting to note that the 25-mo analysis of the 1988 experiment found a very strong negative *Macrocystis* impact at the 8-m site that had not demonstrated a *Macrocystis* or *Pterygophora* effect after 10 mo. In 1993 during the El Niño, *Macrocystis* stipe density had a strong negative effect at both 8-m sites. There was no effect at 15 m south, but a strong negative effect at 15 m north. There were no effects at the deeper sites. It appears that *Laminaria* densities at the shallow sites are impacted more strongly by competition with *Macrocystis* than in the deeper sites. In addition to *Macrocystis*, we analyzed for an effect of *Pterygophora* density on *Laminaria* density (Table 5). These correlations were interesting, because some

were strongly positive. In 1988, there were no effects at 8 or 15 m, but at 21 m, where there had been no *Macrocystis* effect, the *Pterygophora* had a strong positive correlation. In 1993, there was a strong positive *Pterygophora* effect at 8 m south, but not at 8 m north or the deeper depths. *Survivorship*.—In 1988, the *Macrocystis* effect was so severe at 8 m that no *Laminaria* survived more than 32 wk (Fig. A16 in the Appendix). There was a strong negative impact at 8 and 15 m, but not at 21 m (Table 1). However, the much thinner *Macrocystis* density during the El Niño in 1993 had no significant effect on *Laminaria* survivorship, although one of the 15-m clearings showed a strong relationship; the differences

between the clearings may have reflected a *Desmarestia* effect (Dayton et al. 1992), although the *Desmarestia* was gone by September 1993.

Growth.—Data from the 1989 seasonal growth peak of tagged *Laminaria* (Fig. A17 in the Appendix) were used in the analysis (Table 5). There was a very strong negative *Macrocystis* impact on growth at both 15 and 21 m. Except for 15 m north, in 1993 the negative effects were also important at all three depths.

Interspecific competition with *Pterygophora* also appeared to affect *Laminaria* growth rates, at least under certain conditions (Table 5). Interestingly, in some cases, the effects were positive, and, in other cases, they were negative. In the La Niña experiment, there were very strong positive effects of *Pterygophora* density at both 15-m sites, but an equally strong negative effect at 21 m. In the 1993 El Niño experiment, neither 8-m site had a *Pterygophora* effect, possibly because the *Macrocystis* effect had been so strong on both *Laminaria* and *Pterygophora*. The 15 m south site had a strong negative *Pterygophora* effect, but there was no effect at 15 m north. In addition, the 21 m north site had an important negative correlation between *Pterygophora* and *Laminaria* densities, but in contrast the deeper 23-m sites had strong positive *Pterygophora* correlations with *Laminaria* growth.

Reproduction.—Reproductive effort is highly seasonal, but it also has a great deal of spatial and inter-annual variability (Fig. 8; Fig. A18 in the Appendix). Generally, there was an order of magnitude difference in the mean percent soral cover between the two experiments (Table 5), with the reproductive effort in *Laminaria* much higher in the second (El Niño) experiment. Probably because of the uniformly severe interspecific competition, there were no important depth effects during the La Niña, although the 21-m site showed a strong negative *Macrocystis* effect. There were some big differences between depths during the El Niño, although they were not consistent through time. For example, one could argue for a depth effect in winter 1994, but this was reversed the following year. In addition, there was considerable summer reproduction at 8 m in both 1994 and 1995, but none elsewhere. Moreover, these patterns do not behave consistently within a depth profile. In fact, *Laminaria* reproduction in the north clearing at 15 m was always higher under the high density than under the low density *Macrocystis*. There were no *Macrocystis* or *Pterygophora* effects on *Laminaria* reproduction deeper than 8 m during El Niño. Also, since *Laminaria* recruited later at 21 and 23 m, their first reproductive season was a year later than at 8 and 15 m. A *Macrocystis* effect was observed only at 21 m in 1988, and there was a negative *Pterygophora* effect at 8 m north.

Canopy-thinning and clearance experiments:

IV. Effects of *Macrocystis* and/or *Pterygophora* on *Eisenia*

There were enough naturally recruiting *Eisenia* at 8 and 15 m in 1991 to measure survivorship, growth, and

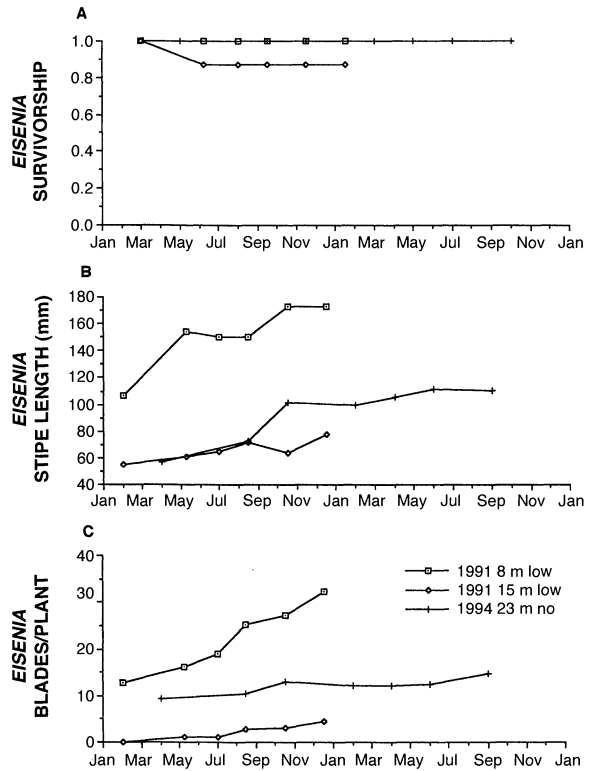


FIG. 10. (A) Survivorship of naturally recruited *Eisenia* in the 8-m low-density *Macrocystis* treatment and in the 15-m low-density *Macrocystis* treatment, 1990–1991, and in the 23-m clearing with no *Macrocystis* in 1994. (B) Mean stipe length of naturally recruited *Eisenia*. (C) Mean number of sporophyll blades of naturally recruited *Eisenia*. Note that the data for the 1991 cohort were collected for 11 mo.

reproduction (Fig. 10). No *Macrocystis* effect could be determined, because *Eisenia* recruitment was observed only in the low-density *Macrocystis* treatments at each depth. This in itself may be indicative of an effect of the *Macrocystis* canopy on the irradiance needed for *Eisenia* recruitment. Some interesting depth effects were again apparent in 1994 as *Eisenia* recruitment occurred only in the 23-m clearing that had no *Macrocystis*.

Survivorship, bifurcation, and growth.—For at least the first 11–21 mo, there was growth and very good survivorship of the three sets of tagged *Eisenia* (Fig. 10). Those at 8 m experienced no mortality, and, after only 2–4 mo, two of the six plants had bifurcated (unpublished data). After 6–8 mo, all *Eisenia* had bifurcated. The time to bifurcation was much longer at 15 m: after 8 mo, only one of seven plants had bifurcated; and after 17 mo, only two of the seven had bifurcated. In 1994, five of the 12 plants at 23 m had bifurcated after 11 mo. Because *Eisenia* recruited at 8 and 15 m at the same time in late fall 1990, initial stipe growth could be compared, and it was much higher at 8 m (Fig. 10). Mean total stipe length of plants at 8 m was almost twice that at either 15 or 23 m.

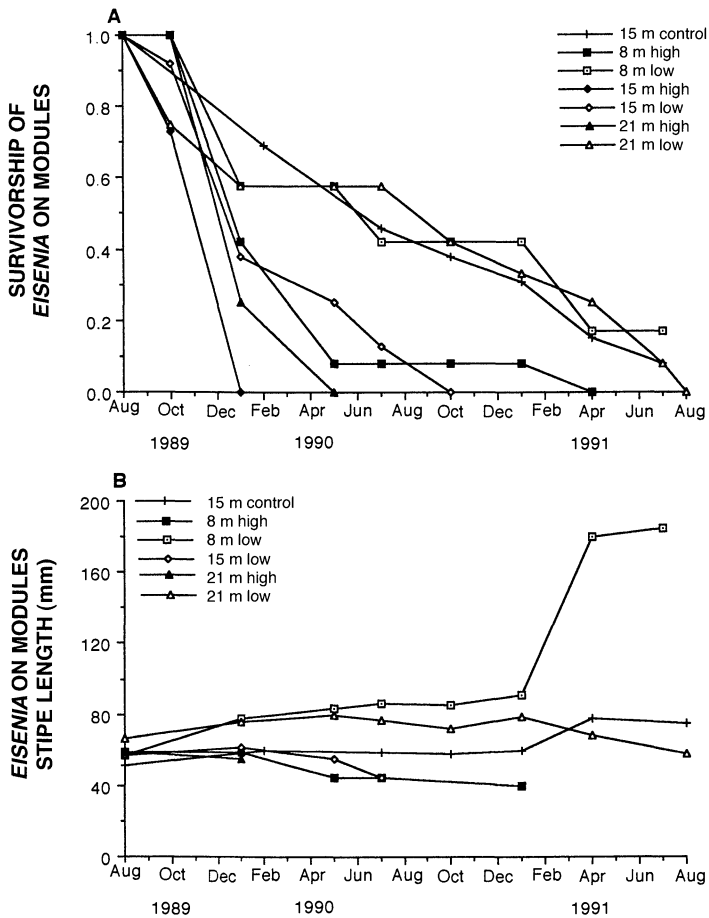


FIG. 11. (A) Survivorship of *Eisenia* transplanted on modules to high- and low-density *Macrocyctis* treatments in the clearing experiments, 1989–1991. Survivorship of *Eisenia* in a control population at 15 m is also plotted. (B) Stipe length of *Eisenia* transplanted on modules and in the 15-m control.

Reproduction.—*Eisenia* at 8 m also had a higher reproductive output as measured by sporophyll blade production (Fig. 10). Not only did plants at 8 m produce more sporophylls, but the rates at which these blades were produced was higher than at 15 or 23 m. Interestingly, while sporophyll production was higher at 23 m in 1994 than at 15 m in 1991, the rates at which new blades were produced were very similar. The number of blades with sori per plant also showed a marked depth effect. During winter 1991–1992, two of six plants at 8 m actually produced sori. During winter 1992–1993, all six became reproductive. Plants at 15 m never became reproductive. At 23 m in 1994, only two of the 12 plants had become reproductive after 13 mo.

Module experiments

Survivorship.—Even though survivorship of *Eisenia* transplanted on modules in 1989 was not as good as controls, some important *Macrocyctis* and depth effects were apparent (Fig. 11A). The greatest mortality occurred during the first winter: at each depth, there were significant *Macrocyctis* stipe effects on the number of weeks that the *Eisenia* survived (Table 6). Plants at 8 and 21 m low-density *Macrocyctis* and the control

plants at 15 m had the highest survival, while no plants survived after only 9 mo in the high-density *Macrocyctis* treatments at 15 and 21 m. The *Macrocyctis* treatment effect appears to be much more important than the depth effect on survivorship, as plants in the high-density *Macrocyctis* treatments, at all three depths, were unhealthy and had high mortality.

Stipe growth and bifurcation.—The *Eisenia* on modules in the 8-m low-density *Macrocyctis* site appeared to be the healthiest. Two of the plants at 8 m low-density *Macrocyctis* had bifurcated after 6 mo, and, after 17 mo, three of five had bifurcated. No other plants had bifurcated by that time. Mean total stipe length of plants at 8 m low after 17 mo was $>2\times$ that of the remaining plants at 21 m as well as the 15-m controls (Fig. 11B). These data were compared with nearby control situations. The mean percent growth (percent growth = $[\text{stipe length} - \text{original length}] / [\text{original length}] \times 100$) of *Eisenia* at 15 m was 62% of the original stipe length, compared with the control plants, which exhibited 17% growth, after 14 mo. After 21 mo, the *Eisenia* in the 8 m low-density *Macrocyctis* grew 228%, while the 15-m control plants grew only 47%.

Effects on articulated coralline and foliose red algal cover.—The turf of articulated coralline algae was re-

corded as percent cover of the substrate; it responded differently in each experiment and demonstrated higher cover in shallow water (Table 7). There was only one important effect of *Macrocystis* stipe density on percent cover of articulated coralline algae after 10 mo in the 1988 experiment at 8 m (Fig. A19 in the Appendix). There were no *Macrocystis* effects at 15 or 21 m. After 25 mo during La Niña, there were very prominent negative *Macrocystis* effects at 8 and 15 m. This suggests lag effects for the coralline algae. There were no *Macrocystis* effects on articulated coralline cover during the 1993 El Niño. Neither were there any effects of *Pterygophora* density on percent cover of articulated coralline algae, except during 1988 at 8 m.

There were evident effects of *Macrocystis*, but not *Pterygophora*, on the cover of foliose red algae (Fig. A20 in the Appendix) during the El Niño experiment (data were not collected during the La Niña), and *Macrocystis* had important negative effects at both 8-m sites (Table 7). There were heavy patches of *Desmarestia* that may have obscured the initial recruitment and abundance differences (Dayton et al. 1992). Finally, there was a strong *Macrocystis* impact at 23 m.

DISCUSSION

This paper is predicated on the assumption that fitness and community organization are based on the net effects of many types of environmental factors that influence the distribution, abundance, survivorship, growth, and reproduction of the component species. Kelps have evolved in the context of great natural variation in oceanographic climate as well as many types of biotic interactions. Here we have attempted to evaluate kelp populations in the context of integrated and interacting oceanographic and biological processes.

Oceanographic processes influence marine systems over many scales (Hauray et al. 1978, Barry and Dayton 1991). This is certainly true in coastal ecology, as efforts to generalize from even widely accepted models in the marine coastal zone, such as those of Connell (1961) and Paine (1966), are proving illusory and certainly not general in time or space (Connell 1970, Paine 1994; see recent review in Dayton 1994 for many hard substrata examples, and Hall et al. 1994 for soft substrata examples). The strong influence of oceanographic processes over large scales is especially true of kelp systems (Dayton and Tegner 1984b, Tegner et al. 1996, 1997). Santelices (1990) makes a strong case that "the processes of reproduction, dispersal and recruitment of seaweeds often involve different ecological scales . . ."

Most interesting ecological questions occur at regional scales far larger in time and space than those used in controlled ecological experiments. There have been very few attempts to scale up small-scale research to these larger, but more important, scales in time and space (Thrush et al. 1997). Obviously, there are many practical reasons to work at small scales with the as-

sumption that the processes have some generality in space and time; however, such assumptions are rarely tested. Small-scale experiments, no matter how well replicated, lack important reality; unless they are built on a substantial foundation of natural history, including an appreciation of variability of patterns in time and space as they affect recruitment, density, survivorship, growth and reproduction rates, and dispersal. To understand larger scale patterns, it is necessary to integrate empirical small-scale experimental studies into the large-scale mosaic (Wiens 1993, Root and Schneider 1995, Thrush et al. 1997). How can we scale up small-scale studies of patterns and processes in a kelp habitat to contribute to a general understanding relevant over larger and longer scales?

One solution is to create large-scale experiments such as whole watersheds (Likens 1985) or lakes (Schindler 1987, Carpenter et al. 1995). In most cases, controls and replications are precluded, as often is standard statistical analysis. The problem of scaling up from experiments is acute, because most experiments can not be formally generalized (Eberhardt and Thomas 1991). Various methods of formally cycling experiments and surveys have been recommended by Rastetter et al. (1992) and Wiens et al. (1993). Schneider et al. (1997) and Thrush et al. (1997) have presented examples of iterative cycling between models, observations, and experiments.

We have evaluated the "fundamental niches" (sensu Hutchinson 1957) of important species of kelp with long-term observations and experiments that have incorporated different oceanographic conditions with contrasting levels of nutrients and disturbance. To understand the spatial components of the fundamental niches and to explore the relative importance of these variables across an environmental gradient, we have replicated these observations and experiments at different water depths in the kelp forest. The "realized niches" resulting from biotic interactions were evaluated by simple density manipulations over both time and space. Santelices (1990) reviews many studies demonstrating intense intra- and interspecific density effects. For several species of kelps, we have evaluated survival of recruits and juveniles, as well as their growth and reproduction in different oceanographic climate conditions, types of disturbance, and important competition. Because the different oceanographic conditions have presumably included important differences in nutrients, we are able to evaluate the importance of bottom-up (nutrients and light) forcing on these relationships. Moreover, because we have also experienced extreme variation in the intensity and extent of physical disturbances over almost 30 yr, we can contrast important components of top-down (biotic and abiotic disturbance) forcing as they influence the relationships under study (Dayton et al. 1992).

Conducting experiments during two very different oceanographic climates over the environmental depth

TABLE 6. Summary of the effects of competition on kelp life history parameters.

Response variable	Depth (m)	Mp effect on Mp			Mp effect on Pc			Mp effect on Lf		
		10 mo, 1988	25 mo, 1988	1993	10 mo, 1988	25 mo, 1988	1993	10 mo, 1988	25 mo, 1988	1993
Density	8				0.0001	0.0050	0.0174	NS	0.0004	0.0208
	8				NS	0.0001
	15				0.0131	0.0623	NS	0.0003	NS	NS
	15				NS	0.0159
	21				NS	NS	NS	NS	NS	NS
	23				NS	NS
l_x	8	...	NS	0.0121	...	NS	NS	...	0.0001	NS
	8	NS	0.0001	NS
	15	...	NS	NS	...	0.0276	NS	...	0.0001	0.0580
	15	NS	NS	NS
	21	...	NS	NS	...	No Pc	NS	...	NS	NS
	23	NS	No Pc	NS
Growth or stipe growth	8	0.0004	0.0448	NS	0.0001	†	0.0294	†	...	0.0148
	8	NS	0.0001	0.0001
	15	0.0001	0.0001	NS	0.0001	†	0.0001	0.0001	...	0.0001
	15	NS	0.0002	NS
	21	0.0535	NS	NS	No Pc	No Pc		0.0001	...	0.0103
	23	NS	No Pc	0.0009
Holdfast size	8	0.0001	0.0004	0.0096						
	8	NS						
	15	0.0001	0.0001	0.0879						
	15	0.0481						
	21	0.0001	0.0026	NS						
	23	0.0801						
Sporophyll production	8	0.0001	0.0047	NS	0.0001	†	0.0004			
	8	NS	0.0001			
	15	0.0001	0.0001	0.0391	0.0001	†	0.0001			
	15	0.0536	0.0134			
	21	0.0001	0.0104	NS	No Pc	No Pc	0.0430			
	23	NS	No Pc			
Sori production	8	0.0041	NS	NS		...	NS	†	...	NS
	8	NS	0.0001	NS
	15	0.0156	0.0164	NS		...	0.0017	NS	...	NS
	15	NS	NS	NS
	21	0.0030	NS	NS		...	NS	0.0001	...	‡
	23	0.0005	No Pc	NS

Notes: P values for the effects of the independent variables, *Macrocystis* stipe density and *Pterygophora* density are presented if <0.10. Mp = *Macrocystis pyrifera*, Pc = *Pterygophora californica*, Lf = *Laminaria farlowii*, Ea = *Eisenia arborea*; NS = not significant ($P > 0.10$). No data are available for empty blocks in the table.
† Could not perform analysis because of 100% mortality in the high *Macrocystis* treatment.
‡ No *Laminaria* reproduction had occurred by the time plants elsewhere were reproductive.
§ Could not perform analysis because modules in one treatment were lost.
|| No peak present.

gradients of one of the largest giant kelp forests in the world allows an unusual evaluation of the robustness of competition experiments in time and space. This community is characterized by a single strong competitive dominant plant, *Macrocystis pyrifera*, and several understory species, especially *Pterygophora californica*, *Eisenia arborea*, and *Laminaria farlowii*. Previous work (Dayton et al. 1984) has shown a competitive hierarchy of *Macrocystis* > *Pterygophora* > *Laminaria* and other understory species including red foliose and coralline algae, and that the hierarchy changed in different regimes of wave exposure. The current study has demonstrated that the intensity of that pattern varies markedly across depth in the same region.

Perhaps our most striking observation is the role of

scaling in time. Santelices (1990) and Reed et al. (1996) summarize the literature, emphasizing the important role of seasonal patterns in reproduction. Certainly, we observed seasonality in *Pterygophora* and *Laminaria*. However, longer scales in time seem even more important, as long-term research demonstrates the critical role of oceanographic climate that varies from the nutrient-poor conditions of massive, or even intermittent, El Niño conditions (such as we studied in 1992–1993 in which the competitive dominant was highly stressed) to a nutrient-rich La Niña event (in which the competitive dominance was very powerful) (Dayton et al. 1992, Tegner et al. 1996, 1997). A historical review (Tegner et al. 1996) reports major changes in the *Macrocystis* canopy over the last century, and up to two-thirds reductions in standing biomass and stipe carrying

TABLE 7. Summary of the analyses of the effects of *Macrocystis* stipe density on the cover of articulated and foliose red algae using Generalized Linear Modeling. Effects of *Pterygophora* were examined by using *Pterygophora* density as a second independent variable in the analyses.

Response variable	Initial year	Depth (m)	Error (df)	After 10 mo				After 25 mo				
				<i>Macrocystis</i> effect		<i>Pterygophora</i> effect		<i>Macrocystis</i> effect		<i>Pterygophora</i> effect		
				Probability (P)	Regression coefficient	Probability (P)	Regression coefficient	Error (df)	Probability (P)	Regression coefficient	Probability (P)	Regression coefficient
Articulated coralline algae (cover)	1988	8	3	0.0001	−0.24	0.0003	−0.03	4	0.0001	−0.14	NS	...
		15	3	NS	...	NS	...	4	0.0001	−0.26	NS	...
		21	3	NS	...	NS	...	4	NS	...	NS	...
	1993	8 south	6	NS	...	NS	...					
		8 north	6	0.0007	−0.03	NS	...					
		15 south	7	NS	...	NS	...					
		15 north	7	NS	...	NS	...					
		21 south	NS	...					
		21 north	3	NS					
		23 south					
23 north	3	NS	...	NS	...							
Foliose red algae (cover)	1988	8							
		15							
		21							
	1993	8 south	7	0.0572	−0.02	NS	...					
		8 north	7	0.0001	−0.06	NS	...					
		15 south	7	NS	...	NS	...					
		15 north	7	NS	...	NS	...					
		21 south					
		21 north	3	NS	...	NS	...					
		23 south					
23 north	6	0.0214	−0.41	NS	...							

Notes: Separate analyses were performed using data from each clearing at each depth. *P* values for the effects of the independent variables, *Macrocystis* stipe density and *Pterygophora* density, are presented if <0.10; NS = not significant. No data are available for empty blocks in the table.

vorship during the La Niña, but, with one exception, there were no significant intraspecific *Macrocystis* effects on survivorship at any depth during either La Niña or El Niño conditions. The one exception was one of the two shallow clearings in 1993, which may have resulted from localized *Desmarestia* settlement or patchy localized *Macrocystis* recruitment (Dayton et al. 1984). Thus, there was a single shallow-water intraspecific effect of *Macrocystis* stipe density on survivorship during El Niño. There were strong oceanographic and competition-induced differences in growth of both holdfasts and sporophylls, which were highly impacted by *Macrocystis* stipe density at all depths during La Niña, but only at shallow depths where nutrients are more likely to be limiting during El Niño (Table 6; Jackson 1977, 1983, Gerard 1982, Zimmerman and Kremer 1984). Neushul and Harger (1985), working in a very shallow (7-m) protected site near Santa Barbara, found that density manipulations and fertilization of the surface canopy resulted in surprisingly high yields, with a considerable amount of genetic among-plant variation. As in our experiments, they found important density effects. They also found similar nutrient effects (corresponding to our temperature effects) and that fertilization was important only during the warm, “nutrient drought” periods of the

year. Again, consistent with our results, Reed et al. (1996) have shown that nitrogen content of adult *Macrocystis* tissue was negatively correlated with temperature, but positively correlated with reproductive capacity. Summarizing for *Macrocystis*, the intraspecific impacts were mostly restricted to the nutrient-rich La Niña conditions, with a tendency toward being more severe at shallower depths. It is important to point out that there were large background differences in which the nutrient-rich La Niña conditions resulted in increased *Macrocystis* growth and reproduction in general, but that the intraspecific impact was nevertheless very severe during the La Niña.

At smaller (10–100 m²) scales, *Macrocystis* usually had conspicuously patchy recruitment. We suggest that this results from a drifting entanglement of several plants snagged on the bottom for a few days (Dayton et al. 1984) and/or dense but patchy recruitment of *Desmarestia* that restricts kelp recruitment in the area (Dayton et al. 1992). In 1988, for example, *Desmarestia* recruited so densely at 15 m that an entire experimental block was abandoned and a new clearing made nearby. Another *Desmarestia* recruitment event occurred at 8 and 15 m in 1993, and we removed the *Desmarestia* for 4 mo to minimize its impact.

Pterygophora californica

Three enrichment experiments to consider the role of oceanographic conditions on *Pterygophora* were attempted, using the same techniques as Dean and Jacobson (1986) who found enrichment effects with *Macrocystis*. The first was conducted from September 1991–January 1992, when it was terminated by a break in the nearby San Diego City sewage outfall. The second was run from September 1993–February 1994 and was terminated by prolonged strong upwelling in the area that produced cold, nutrient-rich water that made treatment irrelevant. Finally, the third was run from July 1994–December 1994, at which time all the plants were destructively sampled and the soral tissue weighed in the laboratory. In each case, the results were suggestive, but in contrast with Dean and Jacobson's (1986) results with *Macrocystis*, we found no significant differences in growth, sporophyll numbers, number of fertile sporophylls, or wet mass of soral tissue for *Pterygophora*.

Pterygophora is known to be competitively dominated by *Macrocystis* (Dayton et al. 1984, 1992, Reed and Foster 1984, Tegner et al. 1997). *Pterygophora* responded to the loss and poor growth of *Macrocystis* in the 1982–1984 El Niño in many areas (Dayton and Tegner 1984a, Tegner and Dayton 1987, Dayton et al. 1992), but, except for the shallow 12-m site (Fig. 7A), *Pterygophora* recruitment in these sites during the post-1982–1984 El Niño period was quickly dominated by *Macrocystis* (Dayton et al. 1992). *Pterygophora* populations at the more shallow sites were virtually eliminated by the 1988 storm (Dayton et al. 1992). Like *Macrocystis*, the background densities of *Pterygophora* were almost an order of magnitude higher during La Niña.

The effects of *Macrocystis* on *Pterygophora* density, during the 1988 La Niña, were pronounced at 8 and 15 m, but during the 1993 El Niño they were important only at one 8-m site (Tables 1 and 3). The 1988 experiment had much higher initial densities than were observed in the 1993 experiments, but these did not persist. A likely explanation is that we observed extremely heavy recruitment of both species after the 1988 storm, and higher nutrient concentrations during the La Niña contributed to a strong *Macrocystis* canopy impact on *Pterygophora* that occurred later. Another unexpected observation is that in 1994–1995, the north and south clearings at 15 m behaved differently. The south clearing followed the expected negative relationship between *Pterygophora* density and *Macrocystis* stipe density, while the north site had a much lower *Pterygophora* density in the no-*Macrocystis* treatment than in the low *Macrocystis* density. Nevertheless, at the high *Macrocystis* density, the *Pterygophora* density was similar to that of the south clearing, suggesting patchy recruitment. Another natural history explanation for the low *Pterygophora* density

with no *Macrocystis* is that the site had a very heavy cover of *Laminaria*, which we observed to be able to reduce recruitment of both *Macrocystis* and *Pterygophora*, in the 1970s (Dayton et al. 1984), before *Pterygophora* appeared. As mentioned, the 1988 high *Macrocystis* area had a much lower *Pterygophora* density after 25 mo, suggesting that it simply took longer for the *Macrocystis* effect to be exerted.

The most impressive effects of *Macrocystis* on *Pterygophora* were exerted on growth and reproduction, which were very strongly impacted by *Macrocystis* stipe densities at most depths (Table 3). DeWreede (1984) found a clear relationship between biomass and reproductive output for *Pterygophora*, and Novaczek (1984) and DeWreede and Klinger (1988) reported similar patterns for *Ecklonia radiata*, and *Laminaria setchelli* and *L. ephemera*, respectively. This relationship between growth and reproduction was apparent in our study, with both being strongly affected by competition with *Macrocystis*.

Considering the strong general interspecific effects of *Macrocystis* on *Pterygophora* growth and reproduction, it is interesting that we did not find strong effects on survivorship. The only *Macrocystis* effects on survival were at 15 m during the La Niña and at 8 m during the El Niño (Tables 1 and 3). The module experiment (Table 4) also recorded a strong negative effect on survivorship at 15 m. We believe that this lack of consistent and strong effect on survival is an artifact that is caused by a lag in time before the *Pterygophora* die; spindly *Pterygophora* were slow to die even if they could not grow or reproduce. *Pterygophora* on the transect lines (Fig. 7) disappeared by 1992, a year after we stopped monitoring the 1988 clearing experiment. Similarly, Reed (1990) found *Pterygophora* survival was not density dependent, probably for the same reason. It appears that *Pterygophora* can persist in low light, nutrient-rich conditions, but growth and reproduction are much reduced in low light situations.

These "sublethal" effects are consistent with observations by Reed (1990) and Reed et al. (1996). Reed (1990) documented important intraspecific density dependence in *Pterygophora* growth and reproduction, and related these effects to competition for light. Initial densities of *Pterygophora* in our 1988 experiments were much higher than in 1993, suggesting that the intraspecific effect at 8 and 15 m would be stronger in 1988–1989. It was significantly positive in 1993 in the clearing experiments (Tables 3 and 6), and the module experiments (Tables 4 and 6) also included several examples of strong *Pterygophora* intraspecific competition. Perhaps the most important observation is that *Pterygophora* did not recruit as well at the beginning of the 1993 experiments as they did after the 1982–1983 El Niño storms and after the 1988 storm (Dayton and Tegner 1984a, Reed et al. 1988, 1996, Dayton et al. 1992, Tegner et al. 1997). *Pterygophora* responded quickly at 8 m, but took longer at 15 m. It is not clear

why *Pterygophora* did not respond to the clearings immediately in 1993, although *Desmarestia* at 15 m and limits to dispersal seem to be obvious hypotheses because populations were depressed throughout the kelp forest, and there was no major storm. Furthermore, light levels were very low (Fig. 4). The module experiment did suggest patchy but intense intraspecific competition; this competitive intensity appears to fall off during nutrient-poor years. However, in contrast to Dean and Jacobson's (1986) results with *Macrocystis*, our experiments failed to document nutrient stress in *Pterygophora*, despite repeated efforts. This is consistent with Reed et al. (1996) as well as with our observations of heavy recruitment, growth, and survivorship of *Pterygophora* during the highly nutrient-stressed El Niño of 1982–1984 (Dayton and Tegner 1984a, Tegner and Dayton 1987). Any kelp can be stressed by low nutrients, but *Pterygophora* seems relatively robust and tolerant to nutrient stress.

Laminaria

Macrocystis had variable impacts on *Laminaria farlowii* (Table 5). There were highly significant shallow-water impacts on density during both La Niña and El Niño, but these were not observed in the deepest sites. This probably reflects the denser shallow-water *Macrocystis* canopy. There were strong shallow-water effects on survivorship during the La Niña, but not during the El Niño, and strong effects of *Macrocystis* on *Laminaria* growth at all depths and during both time periods. We also observed effects on reproduction. There were significant *Pterygophora* effects on *Laminaria* density at 15 m only during El Niño, again suggesting that biological interactions are stronger in shallow water. The dense 1988 *Macrocystis* eliminated *Laminaria* at 8 m high density, but there were also highly significant *Pterygophora* effects on *Laminaria* growth in 1988. This significant *Pterygophora* effect was seen only at the deepest site during El Niño. Thus, both *Macrocystis* and *Pterygophora* had serious impacts on *Laminaria* during the nutrient-rich La Niña years. The deeper *Laminaria* at 18 and 15 m, however, fared better after the massive 1982–1984 El Niño (Fig. 7B) and suffered less in the 1988 storm. Both *Laminaria* and *Pterygophora* responded to the loss of *Macrocystis* after the winter storms of 1982–1983 and after the great 1988 storm (see Dayton et al. 1992). This supports a hierarchical effect in which *Pterygophora* has a strong impact on *Laminaria* in the absence of *Macrocystis* (Dayton et al. 1984). Initial densities of *Pterygophora* in the first experiments were much higher than in 1993, so the intraspecific effects at 8 and 15 m would be stronger in 1988–1989. The positive effects may relate to the fact that the high *Macrocystis* treatments also had high *Pterygophora* densities. Hence, there can be a strong correlation between *Macrocystis* and *Pterygophora*.

The evolutionary implications of the La Niña event

on *Laminaria* survival and reproduction are striking. None of the tagged plants in the 8 m high *Macrocystis* treatment, and only two of 16 plants in the 15 m high density treatment, reproduced before their early death. *Laminaria* in the high density *Macrocystis* treatment at 21 m had better survivorship, but only one plant was ever observed to be reproductive at that site. The fundamental niche of *Laminaria* is very broad, as evidenced by its large geographic range as well as its extremely wide depth distribution ranging from the intertidal to 120 m (Lissner and Dorsey 1986). But, because it is so sensitive to competition, its realized niche is relatively small; and an extended period of colder temperatures, by stimulating overstory species, could be devastating for this competitively inferior member of the understory.

Eisenia

Eisenia arborea has as wider depth distribution than *Pterygophora*, but it also ranges south down the western Baja California peninsula. Compared with the other kelps we have studied, recruitment rates of *Eisenia* were extremely low, and we observed it only in shallow low *Macrocystis* treatments or in deeper areas that had no other canopy. This low recruitment has been consistent over the entire 27 yr that we have worked at Point Loma. Once juveniles were established, there was remarkably good survivorship (Fig. 10). Both growth and reproduction were much diminished with depth; stipe growth at 8 m was ~2× that observed at deeper depths, and sporophyll production was much higher in shallow water. These conclusions are consistent with the module experiments, in which the low density treatments had significantly higher survivorship at all three depths (Table 6), and the only growth was observed in the shallow low density treatment (Fig. 11). The *Macrocystis* treatment effect seemed much stronger than the depth effect.

Like *Laminaria*, *Eisenia* seems especially sensitive to competition in almost all life history parameters. Recruitment is strongly inhibited by canopies, as are growth and reproduction. Most interestingly, it seems to be the slowest kelp of those studied to reach sexual maturity. This was not expected, because it has a very broad depth distribution occurring in deep water (Lissner and Dorsey 1986) as well as into the intertidal at Point Loma (Dayton et al. 1992). Perhaps these fringe populations serve as refuges from competition. It is important to point out that although recruitment is very rare and seemingly sensitive to competition, in the 1970s and early 1980s we observed *Eisenia* to have high survivorship and to strongly out compete *Pterygophora* in the 15 m patches (Dayton et al. 1984).

CONCLUSIONS

It seems that the strongest biological interactions were consistently seen during the La Niña, when nutrient-rich water conditions resulted in strong canopy

growth, especially in shallow water. This resulted in significant and often massive competitive impacts on the subordinate species. These patterns were dependent upon the depth of the research sites, because stipe carrying capacity increases with decreasing water depth (Dayton et al. 1992), resulting in denser *Macrocystis* canopy growth in shallow water. These patterns were very different during the nutrient-poor El Niño years, when the *Macrocystis* canopy was more strongly impacted than the understory canopies (Dayton and Tegner 1984a, Tegner and Dayton 1987, Tegner et al. 1996, 1997). In terms of the fundamental and realized niches of the kelps, the fundamental niches were strongly influenced by light and nutrients, but the realized niches that were potentially dictated by canopy competition were variable in time, depending upon the oceanographic climate (ENSO events).

Recovery from the two oceanographic climate events was also different. Patches and populations of kelps all recovered from El Niños remarkably quickly, however, the recovery from the strong canopy competition induced by the nutrient-rich La Niña was much slower and some of the patches appear to be permanently changed. Understory patches at 15 m that had persisted 25 yr through the strongest El Niño in a century and perhaps the most destructive storm in two centuries (Dayton et al. 1992) were finally eliminated by light limitation induced by La Niña conditions. Indeed, *Laminaria* disappeared from large areas. This emphasizes the long-term persistence of rare competition (both intra- and interspecific) events.

Most reviews of disturbance emphasize the importance of the intensity and scales of the perturbation. Kelp forests are exposed to a large array of small-scale disturbances, many of which have been well studied (Dayton 1985); however, integrated studies of large scale events are rare (Dayton et al. 1992, Tegner et al. 1996, 1997). Concerning the disturbances impacting Point Loma in the 1980s, one effect was increased canopy destruction. However, much of the structure of the community recovered quickly (Dayton et al. 1992). Tegner et al. (1997) discussed how the patterns of succession following the El Niño storms of 1982–1983 and the single 1988 storm were very different because of the different oceanographic climates that followed the disturbances.

Age of maturation is one of the most important demographic parameters. The *Macrocystis* density treatment had little intraspecific or interspecific effects on this parameter, except for *Pterygophora* during La Niña and the shallow site during the El Niño. However, very important depth effects during La Niña were only marginal during El Niño years. Santelices (1990) summarizes some of the literature describing ontogenic patterns of reproduction. Most authors (e.g., DeWreede 1984, Chapman 1986a, Reed 1987) agree that the most important determinant of the actual number of spores produced is the size of the plant, rather than the age

of maturation. However, age of maturation is well known to be an important component of an organism's response to disturbance. Santelices (1990) points out that age can be a poor indicator of demographic parameters for kelps, because growth and reproductive rates can be suppressed by environmental variables, like those that we have demonstrated.

What is the selective mechanism for the different reproductive strategies of kelps in this community? Survivorship of *Macrocystis* and *Pterygophora* appear similar in our results, *Pterygophora* is well known to be able to live much longer than *Macrocystis* (Dayton 1985). Reed et al. (1996) suggested that *Macrocystis* reproduces more or less continuously, because it is energetically cheap to produce spores; and, considering that the plants do not live very long, it is adaptive bet-hedging to reproduce continuously rather than risk mortality. On the other hand, the often much longer lived *Pterygophora* can afford to save their energy and reproduce when the probability of spore survival is highest. Reed et al. (1996) observed that *Pterygophora* spore C/N ratios were constant over time, whereas the *Macrocystis* C/N ratio was strongly affected by water temperature, which is an indicator of nutrients. Our data support this observation: the important storm disturbances we have documented since 1970 occurred in the winter months, with consequent increased irradiance on the bottom (summarized in Dayton et al. 1984, 1992). Furthermore, *Pterygophora* reproduction (Fig. 8B) peaks before the onset of cold temperatures during the spring (Fig. 2), offering further indication that reproduction in this species is independent of nutrients. Not surprisingly, *Pterygophora* seems sensitive to the amount of irradiance for reproduction (Reed 1990, Reed et al. 1996), and this strongly selects for seasonal reproduction during the period most likely characterized by disturbance, and subsequent open space on the bottom, as well as storm-thinned canopies above. In contrast, as we have seen, *Macrocystis* is extremely sensitive to nutrient stress (see also Neushul and Harger 1985, Reed et al. 1996, Tegner et al. 1996, 1997). Because its canopy floats on the surface, adult *Macrocystis* are sensitive to surface nutrients and relatively less sensitive to light, thus decoupling surface and benthic events.

Demonstration that the most lasting impacts of natural variation in oceanographic climate result from those induced by strong light competition suggests revisiting the comparison between density-dependent/density-independent regulation and density-vague relationships (Strong 1986). In density-vague relationships, inconsistent relationships are occasionally replaced by strong density-dependent impacts, such as those resulting from competition for light, which are strengthened by the nutrient-rich La Niña. It appears as though the realized niches (as opposed to the fundamental niches) are defined by density-vague regulation. For example, most small-scale studies of kelp have shown density-dependent regulation of growth

and reproduction (see reviews in Dayton 1985, Chapman 1986b, DeWreede and Klinger 1988), and self-thinning of dense patches of new recruits (Dayton et al. 1984) is common. Much less common, but extremely important in a density-vague sense, are the strong and more lasting events of competitive exclusion, such as seen in this study.

Finally, ecosystem biologists ask questions about environmental parameters critical to the very existence of the system as a whole. For example: what controls productivity and various rate functions, and what general forcing functions work to channel material through different pathways? While these parameters define the biotic systems, it has been difficult to relate ecosystem variables to evolutionary processes. We and Tegner et al. (1996, 1997) have evaluated temperature as a surrogate of nitrogen and light, two of the most important parameters affecting kelp productivity. We found that temporal differences in nitrogen affect the growth rate of the dominant kelp. Furthermore, there are cascading effects on the recruitment, survivorship, and reproduction of the understory species, and these effects vary across the depth gradient. That is, the availability of nutrients influences kelp interactions across spatial scales, as well as influencing the amount and direction of intraspecific and interspecific competition. This implies that the bottom-up forcing of nutrient availability may be one of the most important characteristics of this system.

What is the appropriate scale of study? For marine systems, this answer must be based on integrating an understanding of the appropriate oceanographic structure or physical processes (Barry and Dayton 1991) with locally important biological processes. The relevant physical and biological processes define both large- and small-scale patterns (Thrush et al. 1997), and these processes should be identified a priori. In our system, small-scale patterns are driven by processes (competition, disturbance, dispersal, etc.) that are also potentially very important at larger scales; however, our most lasting effects result from very large-scale, low-frequency episodic changes in nutrients, with cascading competitive consequences to the other algal populations on in the community.

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APPENDIX

Figs. A1–A20 showing supplemental plots of experimental data are available in ESA's Electronic Data Archive: *Ecological Archives* M069-003.